Conservation Biology

Foundations, Concepts, Applications

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Second Edition

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ISBN 978-1-4020-6890-4 e-ISBN 978-1-4020-6891-1

Library of Congress Control Number: 2007942036

Printed on acid-free paper

9 8 7 6 5 4 3 2 1

springer.com

Cover Photograph Description

Wiwik is a citizen of Indonesia, currently completing her BA degree in psychology. Her professors think she is an excellent student, but Wiwik is featured on the cover of this textbook for another reason. She works as a caregiver to orphaned orangutans at the Nyaru Menteng Orangutan Rehabilitation Center in Indonesia's Kalimantan province. The orangutan (*Pongo pygmaeus*) is listed by the World Conservation Union (IUCN) as an endangered species. The greatest threat to current populations, now confined to the island of Borneo, is tropical deforestation. But orangutan populations are also threatened in another way. The demand for infant orangutans in the pet trade, and the large sums of money that an infant orangutan can bring on the black market, motivate many people to shoot nursing mother orangutans and sell the infant. Although illegal, many consider the potential gain worth the risk. If caught, the hunter may be fined or sent to jail, but that solves only part of the problem. The infant and now orphaned orangutan has no skills or experience needed to live alone in the forest. Released back to the wild in this state, it would perish.

Because orangutans rely so extensively on learning rather than instinct, they spend 7–8 years with their mothers before becoming independent. To rehabilitate orphaned orangutans, workers like Wiwik educate them in an intensive "curriculum" of foraging techniques, nest building, arboreal locomotion, predator avoidance, and other skills needed to survive in the wild. In our cover photo, Wiwik is showing two 5- to 6-year-old female orangutans, Sirius (next to Wiwik on her left) and Betty (back to the camera) how to open a termite mound and extract the termites from it for food.

Wiwik's efforts are informed by careful scientific studies of orangutan food habits, behavior, social relations, and habitat requirements, but the problem she is attempting to solve, the problem of the conservation of the orangutan, is not, strictly speaking, a scientific question. It is a complex problem that requires an understanding not only conservation science, but of economics, law, ethics, and national and international politics. That is why I chose to make my initial invitation to readers with this picture. It is a picture of the complexity of conservation biology: an international, multi-disciplinary effort in which experiment and management must be combined, and are often blurred, in projects fraught with uncertainty, but not bereft of hope. As this text goes to press, organizations like the Orangutan Conservancy, which administers Nyaru Menteng, are working with the Indonesian government and national and international conservation organizations to make the first successful transitions of these orphaned orangutans into independent, free-living individuals who can again become part of wild populations. It is an effort in which a dedicated worker like Wiwik may have as much to contribute as the world's most famous conservation scientist. And, if there is to be hope for success, it is an effort that will need both. It is also an effort that will need a new generation of conservation scientists, managers, policy makers, and activists if it is to continue. I offer this book as an invitation to the reader, whatever your background and wherever in the world you may be, to learn about this effort, and to join it.

Foreword

I am really delighted that a second expanded edition of this textbook is being printed. The first edition has been useful enough and personally it has been invaluable for my teaching in Latin America. This edition has more international examples and so will appeal to an even wider audience. This is a significant update and revision of a teaching resource of major importance to the teaching of conservation biology.

Conservation is becoming a more urgent discipline day by day as the gravity of the environmental crisis deepens. The reality of climate change is upon us and we know that it is seriously affecting biodiversity in many parts of the world. It is therefore essential to train students based on the large amount of good conservation science that is now available. The author of this text has made a thorough study of this literature and analysed it succinctly and accurately. This text covers both the historic and the most recent developments in conservation. It treats biodiversity as a whole ranging from the species and habitat diversity to DNA and genetic diversity.

The environmental crisis is so great that science alone will not resolve it. It has become a moral and ethical and even a religious crisis. One of the aspects I most like about this text is that as well as treating the practical side of conservation it discusses the philosophical and ethical aspects. It also presents a balanced view of policy and the economics of the subject. If the political and the ethical issues are not addressed we will not win the battle to make the necessary changes that will conserve a major proportion of the world's biodiversity. However, there is also much in this text for the practical field based conservationist.

Fred Van Dyke has done an excellent job of presenting an ever expanding field in an accessible way. The abundant illustrations and the tables are a great help to make the data readily understandable. I urge all students who take up this text to consider all these aspects carefully to prepare you for an exciting career that is vital for the future of our planet.

Ghillean Prance
Director of the Royal Botanic Gardens, Kew, 1988–1999

Preface

In the United States, there is a saying among career politicians. "You're not really an incumbent until you win your first re-election." So in writing textbooks, one is not at all confident of having made much of a contribution after only one edition. The first edition is very educational to the author, but many of the best lessons begin to sink in only after the text is in press, at which point they are too late to benefit the reader.

This second edition of *Conservation Biology: Foundations, Concepts, Applications* reflects some of what I learned from the experience of writing the first edition, both what to do and what not to do, what to leave in and what to leave out. Of course, one not only learns from writing, but from having written. Once a book is released into the world, it takes on a life of its own, and an author learns as much from the responses of his readers as from the research he invested in writing. This second edition is not only informed by new developments in the discipline of conservation biology, but also by the experience of those who have taught the discipline using my text, and I am grateful for their feedback and candor.

Some things are unchanged from the first edition, not only in the book but in the convictions that have motivated me to repeat the effort. I believe, more strongly than ever, that conservation biology should be taught as a unity of thought and practice expressed through a coherent foundation of concepts, theories, facts, and values, not as a loose assemblage of impressive disciplinary expertise. A unified textbook of conservation biology does not attempt to present every subject that conservation biologists have studied, but instead defines the context and relationships of controlling ideas, problems, and applications of the discipline. Critical facts and case histories are important, but they are meaningless without context. We do not remember facts that we memorized years, or even days, ago simply for the purpose of passing a test. Rather, we remember information that skilled teachers imbued with meaning, that inspired and enlightened us, and that led to an understanding of our own discipline, and our place and purpose in it. I have also learned from my colleagues who specialize in the educational process itself (my valued friends in the "Education" department), that effective learners who display high, long-term retention rates of what they have studied learn highly organized information. Ineffective learners with low retention rates learn disorganized information. Therefore, as in the first edition, I have given considerable attention to the organization of ideas in every chapter, and among chapters, so that the organization of ideas is itself part of the way that students will understand the concepts presented. It is the connections of these ideas to one another that matter as much as the ideas themselves.

Guided by these convictions, I have organized this second edition around the same fundamental questions that guided the first edition, questions that I believe give meaning to diverse research and management efforts in all aspects of conservation biology. First, how did conservation biology become a distinct discipline, and what keeps conservation biology from being absorbed into related disciplines? Second, what are the fundamental intellectual, conceptual, and practical problems that conservation biologists must address and solve? Third, what is the role of conservation biology in achieving "success" in conservation in ways that affect all dimensions of the human experience?

So What's New in the Second Edition?

Although these foundational convictions remain unchanged, practical experience with the first edition, my own and my colleagues who used it, has led me to change some specifics. The first edition was encumbered with a strong North American bias, especially in its explanation of the history of conservation and conservation law. Without presuming to have eliminated that bias entirely, I have been intentional in this second edition in presenting the history of conservation, and its legal empowerment and support, in the context of a global conservation community and perspective.

North American examples and experiences have a place in understanding that perspective, but they will no longer be offered as unreflectively or as exclusively as I did in my first effort.

Although the first edition enjoyed course adoptions in over 150 institutions worldwide, even those professors most enthusiastic about the text almost unanimously expressed discontent with the fifth chapter, "The Historic and Foundational Paradigms of Conservation Biology." I have come to agree with that judgment. The paradigm chapter was repetitive, cumbersome, and not well connected to the rest of the text, so I have removed it. Some consideration of historic conservation science paradigms remains important, but these are now dealt with either in the explanation of the history of conservation and conservation biology or in chapters that address more specific topics in genetics, populations, habitats, landscape ecology, or ecosystem management. I have also eliminated the chapter on Restoration Ecology, not because this subject is unimportant, but because restoration manifests itself differently in genetics than it does in landscapes, and so restoration is dealt in these more specific contexts in individual chapters.

As there are elements that have been removed, there are things that have been added. The chapter on conservation genetics and the chapter on the conservation of populations, each formerly presented as a single chapter, have been split into two chapters for each topic. For both genetics and populations, the initial chapter explores the theory underpinning an understanding of their applications in conservation, and a second chapter then gives more detailed examination to specific applications and case histories that make use of such theory. Of course, these kinds of boundaries are invariably leaky, and the reader will find these distinctions expressed more in emphasis than in absolute, uncompromising divisions. In every chapter, old or new, I was blessed with the reviews of highly qualified scientists on specific topics, and, with their help and guidance, I have added examples of the most recent theoretical developments, experiments, and field studies on those topics in each chapter.

Perhaps the most important change for users of the first edition will be the new chapter five, which takes up a topic that was ignored in my first edition. That is the subject of global climate change, its current and projected effects on world biodiversity, and the conservation strategies currently being developed to mitigate those effects. Writing an entirely new chapter is harder than intellectually refurbishing material you have written before, but there was no question that a chapter on climate change had to be included. Readers will judge the quality of the effort, but the intent is simple: to make climate-mediated conservation strategies part of "ordinary science" and discussion in conservation biology. Given the current state of things, I could not do otherwise.

Finally, I take the same risks I took in the first edition in speaking directly to students and prospective future practitioners of conservation biology in the final chapter (Chapter 14). Conservation biology is not practiced by textbooks. It is practiced by conservation biologists. I believe if you want someone to do something, the right and courteous thing to do is to ask them to do it, explain why, and show them the means and resources they will need to succeed. In this second edition as in the first, I have decided to make that appeal directly to my student readers in answering the question: how does one become a conservation biologist?

The Differences in This Book and the Difference It Makes

Like the first edition, this second edition strives to be genuinely interdisciplinary in its approach. Although an understanding of biological facts and concepts is essential and given pride of place, the text takes seriously the contributions of law, political science, economics, ethics, sociology, and other disciplines to the modern conservation effort. Additionally, my book does not conceal issues of ambiguity and uncertainty in conservation science, or issues of controversy in conservation ethics and policy. I do not believe that we should shield students from the inherently controversial, and often contentious, nature of the scientific effort, nor should we try to protect them from the messy uncertainties that inevitably arise when we attempt to translate research results into management decisions. Many years of working with US state and federal conservation agencies, combined with the shared experiences of other conservation professionals from around the world whom I respect, have convinced me that such uncertainty is best acknowledged quickly and forthrightly, lest it lead to recommendations that are more precise than accurate, and produce professionals that are more arrogant than useful. Thus, this second edition, like the first, not only explains, but also critiques the foundational and current practices, techniques, and concepts of conservation biology. My purpose in taking this approach is not to create a spirit of negativism or confusion, but to provoke current and future conservation biologists to examine their foundational premises carefully and make continued efforts to improve all aspects of conservation practice.

I close this preface by noting one other thing that is the same in the first and second editions, but something that only the feedback from the first edition has made me realize that I should explicitly state. Compared to other texts in a variety of disciplines, including conservation biology, my book will often use more direct quotes from primary sources, take more time to explain or dissect an individual case history or theory, or give greater attention to examining the sources or implications of ideas. There is a method to this madness. With my own students, my goal is to teach them ways to think about, understand, and, eventually, critique even the best examples of scientific investigation. I do this because I do not want them to be students forever. I need help. I need their help, and I want them, in time, to become my helpers and, eventually, my colleagues. I cannot accomplish this transformation simply by summarizing the final conclusions of innumerable studies and presenting that distillation as a “list” of things to know, however efficient and time-saving such an approach might be. I must instead attempt to get them to re-create the intellectual process that led to the formation of the conclusion. That takes more time, and requires an emphasis on processing information rather than simply presenting it. For those who believe that the greater the density of information and summary conclusion in a textbook the better, I can only say, with respectful candor, that my book is not the one you should use for that approach. For those who share my commitment to helping students re-create an intellectual process of discovery, insight, and application that, with practice, eventually leads them to form original intellectual creations and applications of their own, I hope you will find this book a useful tool, and I welcome your feedback on how to do it better. I invite all users of this book, whether instructors, students, or inquisitive readers who want to know more about conservation biology, to join me in the adventure of this effort.

Acknowledgements

I am grateful to the reviewers who gave me the benefit of their time, knowledge, experience and expertise to enhance my understanding of all of the topics covered in this text, and to point out my errors of fact and interpretation. I am just as grateful for their insights about teaching, letting me know, from their experience, what works in a classroom and what does not. They have saved me as much embarrassment, and users of the book as much frustration, as they could. Errors and misjudgments that remain are entirely my responsibility. My illustration and permission assistants, Michael J. Bigelow and Lauren Anderson, displayed unflagging patience and fortitude in working with a difficult boss, and amazing creativity in finding ways to transform some of my abstract concepts into tables, graphs and figures that captured concepts elegantly and visually for the students who will use this book. Their pictures often really were worth a thousand words. At Wheaton College, Biology Department Chair Rod Scott, Dean of Natural and Social Sciences Dorothy Chappell, and Wheaton College Provost Stanton Jones were exceedingly gracious and generous in providing me with time, funds, and, at critical moments, much needed encouragement to stick with the work and not give up. I am particularly grateful to Drs. Jones, Chappell and Scott for approving and providing funds, sometimes on very short notice, for this work from the Aldeen Grant program of Wheaton College, and to the college alumni and donors who made such funds possible to support this effort. My editorial assistant Jo Ebihara checked every reference, constructed the index, and developed the glossary with skill and speed, two traits that can be dangerous to combine in most people, but were superbly manifested in Jo. As with my first edition, I continued to be blessed with the world's most capable secretary, Teresa Cerchio Brown, who copied, assembled, and arranged electronic and print material until it had cluttered every part of her computer and office, but never complained and never failed to get everything right. Everyone associated with my new publisher, Springer Science and Business Media, was most helpful and considerate. My editor, Catherine Cotton, worked diligently and patiently to develop our original book proposal and guide it through the process of corporate acceptance and approval. Ria Kanters, Publishing Assistant in Forestry, Ecology, and Conservation in charge of actually assembling my material into a book, displayed the same levels of diligence and patience (perhaps even more patience) in enduring some of my missed deadlines and late-arriving material and assembling it into the present text. Finally I am most grateful to my wife, Linda, who must have thought during some parts of the writing process that her husband had died or run off, since he was rarely seen at home. The end of a thing is better than the beginning, and the end of this book, for now, allows me to look forward to beginning to re-enter something like a normal life.

Fred Van Dyke
Wheaton College
27 September 2007

About The Author

Fred Van Dyke is a professor of biology at Wheaton College (Illinois). He has previously served on the faculties of Northwestern College (Iowa) and the Au Sable Institute for Environmental Studies, as a wildlife biologist for the Montana Department of Fish, Wildlife and Parks, as a scientific and professional consultant to the US National Park Service, the US Forest Service, the Pew Charitable Trust, and to various private environmental and conservation consultants. He is the author of numerous publications on animal home range and habitat use, management and conservation of animal populations, management of successional processes to conserve habitat, and conservation values and ethics.

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The History and Distinctions of Conservation Biology

When the Lady Glanville took an interest in butterflies, this was regarded as so sure a sign of mental imbalance that her will was disputed on that ground.

Martin Holdgate 1999:3

In this chapter you will learn about:

1. **The origins and history of conservation and conservation biology**
2. **The conceptual distinctions of conservation biology**

1.1. Perspectives and Questions for an Inquiry into Conservation Biology

Throughout most of human history, an interest in the conservation of plants and animals, much less a passionate dedication to it, has not been considered a "normal" way of thinking. This is not just the case in ordinary society, but even in the scientific community. Nevertheless, this "different" approach to the natural world, and to science, was given voice and direction at a remarkable meeting in 1978. In that year a group of academic scientists, zookeepers, and wildlife conservationists attended a banquet at the San Diego Wild Animal Park. There biologist Michael Soulé made an impassioned plea to his colleagues: with world extinction rates estimated to be at their highest levels in 65 million years, it was time for academics and conservationists to join forces to save threatened and endangered species (Gibbons 1992). Soulé's words sparked both controversy and criticism, but few were left unmoved. That meeting, now ambitiously called the First International Conference on Conservation Biology, led to new beginnings. A landmark publication that would become a foundational statement of the new discipline's identity, *Conservation Biology: An Evolutionary-Ecological Perspective* (Soulé and Wilcox 1980) resulted, a new scientific organization, the Society for Conservation Biology, was created, and a new discipline, conservation biology, was born.

Officially, the formal organization and incorporation of the Society for Conservation Biology was still some years away. As Soulé noted later,

> *For the record, the Society for Conservation Biology originated about 5 PM on May 8, 1985, in Ann Arbor, Michigan [USA] at the conclusion of the Second Conference on Conservation Biology. An informal motion to organize such a society was approved by acclamation, following reports by chairpersons (Jared Diamond and Peter Brussard) of two ad hoc committees. Those committees met during the conference to discuss the need for such a society and for a journal and I was asked to help from there. With the help of many people and organizations … we drafted a constitution and discussed matters of policy and publication.*
>
> (Soulé 1987:4)

Reflecting on the motives that drew the first members of SCB together, Soulé remarked, "The Society is a response by professionals, mostly biological and social scientists, managers and administrators to the biological diversity crisis that will reach a crescendo in the first half of the twenty-first century. We assume that we are in time, and that by joining together with each other and with other well-intentioned persons and groups, the worst biological disaster in the last 65 million years can be averted. … Although we have varying philosophies, we share a faith in ourselves, as a species and as individuals, that we are equal to the challenge.… For these reasons we join together in professional alliance, in the service of each other, but also in the service of the less articulate members of our evolutionary tree" (Soulé 1987:4–5). Two years after the events Soulé describes, the first annual meeting of the SCB was held at Montana State University in Bozeman (USA) in June 1987.

There were inevitable growing pains. Soulé noted, "The ecologists and biogeographers didn't think geneticists had much to contribute to conservation, and the wildlife managers didn't think that the academic eggheads had anything relevant to say" (Gibbons 1992:20). But, in time, this disparate, cross-disciplinary and international group of scientists learned, not only to speak to one another, but to work together, and to do so with mutual esteem and common purpose. By 2006, membership had climbed to over 11,000 worldwide, the discipline boasted a number of undergraduate textbooks (Hunter 2002; Pullin 2002; Primack 2004, 2006; Groom et al. 2006), dozens of titles on more advanced aspects of conservation problems, and hundreds of colleges and universities offering graduate and undergraduate studies in the discipline. The growth was, in the words of founding member Stanley A. Temple, wildlife ecologist at the University of Wisconsin-Madison, "incredible" (Gibbons 1992). But as science journalist Ann Gibbons noted prophetically over 15 years ago, "…despite the burgeoning funding for conservation biology and the demand from students for more classes in the field, the real test of the vision Michael Soulé elaborated in 1978 is yet to come. The test is not whether conservation biology can convince its academic critics that it is 'real science,' or improve its diplomatic relations with traditional conservationists, or generate funding from federal and private sources. The true test will be whether the field can actually preserve biodiversity" (Gibbons 1992:22).

The intervening years have answered Gibbons first three questions definitively. Throughout the world, in scores of undergraduate and graduate university programs, at the United Nations, in national and provincial government agencies, in non-governmental conservation organizations and citizens groups, in dozens of academic journals and professional meetings, conservation biology is unquestionably recognized as "real science." It has not only improved diplomatic relations with older, more traditional disciplines, but forged many cooperative and cross-disciplinary efforts in a myriad of scientific studies and conservation initiatives. It has generated funding for research and management that now totals in the hundreds of millions of dollars. But the question still remains, as Gibbons put it, that is "the true test." Will conservation biology be able to preserve biodiversity?

Michael Soulé defined conservation biology as a "crisis discipline" whose goal was to provide principles and tools for preserving biodiversity (Soulé 1985). Conservation biology is to biology what surgery is to physiology or war to political science. It must respond to emergency situations with incomplete information, and its goal is a predetermined, desirable outcome, not simply an accumulation of scientific information or an enlightened discussion about interesting problems. Although urgent, short-term goals in conservation change, the long-term goal is the persistence and viability of functioning ecosystems (Soulé 1985). From its inception, conservation biology understood itself as synthetic, eclectic, and multidisciplinary. It did not draw all its theories and models from biology. It had the effect of breaking down the dichotomy of pure versus applied science (Soulé 1985). As an emerging discipline, conservation biology stressed the ***intrinsic value*** of biodiversity (the value of biodiversity in and of itself), not simply its utilitarian values.

Today, nearly 3 decades later, conservation biology is still an arguably new and distinctive discipline, but few, if any, of the major scientific paradigms employed in conservation biology are original, nor are the problems it has attempted to solve. There were conservationists, biologists and conservation dilemmas long before there was conservation biology, and there were many individuals who practiced conservation as biologists. The first question we will attempt to answer is: where do our ideas about conservation come from?

1.2. The Origins of Conservation

1.2.1. Conservation in Historical Context

To understand the origins and history of conservation, one must begin by defining conservation by its goals, not its effects. Human beings always have affected their physical environment and its non-human species, but they have not always been conservationists. A group of people living in equilibrium with their environment is not necessarily an example of conservation, and such people are not necessarily conservationists. They may be very wasteful, but cause no damage because their environment produces more than they need. Or they may be very inefficient, desiring, but unable, to take more from the environment than they do. If their efficiency improves, they will take more, and may do increasing harm to their environment. In this case their "conservation" will be inversely related to their technology. Either way, this kind of conservation will disappear very quickly if the environment becomes less productive or if the people become more efficient at exploiting it (Alvard 1993).

Genuine conservation can occur only when humans knowingly use resources at less than maximum sustainable rates, or forego the use of some resources altogether. This kind of conservation is motivated by appreciating an intrinsic value of the resource itself or from the desire to provide a long-term supply of the resources for others, including others still to come in future generations. These motivations are not mutually exclusive, and they are primarily ethical in nature. Throughout history, human beings have shown themselves to have the ability to embrace both motives, but often have lacked the will to do so. In fact, humans have shown the opposite capacities for intensely selfish motives to get as much of a resource as they can for their own needs and pleasures. The history of conservation is a history of ethical conflict as well as scientific discovery. Conservation has benefits for humans, but it requires restraint and incurs costs. Conservation that involves neither restraint nor cost is not conservation. If one is careless in defining conservation, it is easy to make historical generalizations that are not true. One false historical generalization is that people with little technology are good conservationists and people with high levels of technology are not. Another is that nomadic hunter-gatherer societies conserve the environment and agricultural societies degrade it. This kind of thinking distorts an accurate interpretation of the historical context of conservation.

Throughout the world, early human societies in Europe, Asia, Africa, Australia, and the Americas radically affected their physical environment and the species it contained. They began to "manage" ecosystems even with little technological development, primarily through the use of fire. All early peoples used fire, and with this single tool changed landscapes, exterminated species, and created cultivatable areas (Pyne 2001). Even primitive cultures that can employ effective combinations of fire and cultivation can create significant ecosystem effect. For example, the environmental historian J. R. McNeill noted that "Amazonian peoples apparently painstakingly created their own patches of fertile soil (for farming), the so-called 'dark earths' that make up as much as 10% of the rain forest region" (McNeill 2003:23). Similarly, the place names given to some locations by native North Americans, such as Head Smashed In Buffalo Jump (Pyne 2001:31), attest to hunting methods, with appropriate knowledge of landscape ecology, that contributed to effective population manipulation of selected species, but not for the intention of conserving them. Such population and ecosystem "management" had some of the same effects as conservation management programs today. It altered the distribution of habitats, changed the composition of plant and animals communities, and provided benefits to human beings. But practices of this kind cannot be called "conservation" because they were not used to cause the persistence of, or "conserve" any of the species they affected. This kind of "management" has been correlated with extinctions of large mammals, particularly in North America (Pyne 2001).

Some hunter-gatherer societies did achieve remarkably sustainable and sophisticated forms of resource management that do meet even the most rigorous definitions of "conservation." One such example is found in the allocation of fishery resources among native Alaskans. Although there are five species of salmon (*Oncorhynchus* spp.) (Figure 1.1) that commonly spawn in Alaskan (USA) rivers, the sockeye salmon (*O. nerka*) has long been the most prized by natives. Sockeyes arrive earliest and remain longest in their spawning streams, have the lowest historical variation in annual return numbers, the highest nutritional value and, in the opinion of some, the best taste (Leal 1998). The Tlingit and Haida tribes, two groups of coastal native Alaskan peoples, placed a high value on the sockeye. Sockeye were scarce but definable as property resources because sockeyes migrate only in stream systems that include a freshwater lake. The combination of scarcity and definable resource boundaries enabled the Tglingit and Haida to make rules limiting access to particular streams to an individual clan or house group. Streams were assigned by the *yisatii*, the clan's eldest male, as were limits on how many fish could be taken, and at what times. Management decisions were informed by the *yisati*'s knowledge and life-long experience of both the salmon and the stream, and therefore linked to time- and place-specific knowledge of resource constraint. The *yisati*'s knowledge of family and clan structure also ensured that the number of individuals consuming the resource was appropriate to the sustainable level of production of the resource and based on the size of the stream and the number of people required to set traps and weirs across the stream's mouth. The *yitsati* could use his power to enforce the regulations and to punish violators, but sanctions were rare because fishing rights could not be transferred. As a result, there were few conflicts among users. These conservation practices, and the sockeye salmon they conserved, collapsed in the late nineteenth and early twentieth centuries when other cultures, first Russia and then the United States, ignored the established system and allowed anyone to place traps and weirs at the mouths of rivers.

FIGURE 1.1. The sockeye salmon (*Oncorhynchus nerka*), a species that was historically managed sustainably by the Tginlit and Haida tribes of Alaska through careful division of property rights, site-specific knowledge of habitat and resources, community-based rules of proper fishing methods and site selection, and an intrinsic valuation and appreciation of the sockeye. (Photo courtesy of US National Marine Fisheries Service.)

1.2.2. Cultural Foundations of Conservation

As human societies shifted from hunting and gathering plants and animals to growing and domesticating them, they continued to "manage" nature, but seldom did they in any sense conserve it. In ancient Greece, an advanced pastoral and agricultural society, Plato compared the present land conditions he observed to the past in one of his Dialogues through the character Critias. Critias, in a conversation with Socrates, laments of the land that

> *[O]f old its yield was most copious as well as excellent. … By comparison with the original territory, what is left now is, so to say, the skeleton of a body wasted by disease; the rich, soft soil has been carried off and only the bare framework of the district left. … There were also many other lofty cultivated trees which provided unlimited fodder for beasts. Besides, the soil got the benefit of the yearly 'water from Zeus,' which was not lost, as it is today, by running off a barren ground to the sea; a plentiful supply of it was received into the soil and stored up in the layers of nonporous potter's clay. Thus the moisture absorbed in the higher regions percolated to the hollows, and so all quarters were lavishly provided with springs and rivers. Even to this day the sanctuaries at their former sources survive to prove the truth of our present account of the country.*
>
> (Hamilton and Cairns 1961:1216–1217)

Before Plato, Judaism extended the principle and command of Sabbath, or appointed rest, to include the land. Israel recorded God's command, through his prophet Moses, that the land must receive a rest from cultivation every seventh year.

> *...in the seventh year the land is to have a Sabbath rest, a Sabbath to the Lord. Do not sow your fields or prune your vineyards. Do not reap what grows of itself or harvest the grapes of your untended vines. The land is to have a year of rest.*
>
> (The Bible, Leviticus 25:4–5, New International Version)

The Israelites, like the Greeks, abused their land and did not keep this commandment, but it was not forgotten. Israel's prophets stated that failure to observe the land Sabbath was one of the reasons for Israel's eventual exile from Palestine. Speaking of the defeat of Judah and the destruction of Jerusalem by Nebuchadnezzar in 586 BC, the writer of the Second Book of Chronicles records that Nebuchadnezzar *carried into exile into Babylon the remnant, who escaped from the sword, and they became servants to him and his sons until the kingdom of Persia came to power. The land enjoyed its Sabbath rests; all the* *days of its desolation it rested, until the seventy years were completed in fulfillment of the word of the Lord spoken by Jeremiah* (The Bible, II Chronicles 36:20–21, New International Version).

In China, the practice of setting aside “sacred” or *fengshui* forests around every village, first developed over a thousand years ago during the Song Dynasty (AD 960–1279), was part of a religious practice that attempted to create a spatial framework that would positively regulate spiritual power inherent in the physical landscape, promoting harmony between human and heavenly realms. Such a practice had important practical implications. As one family genealogy from Sichuan notes, “When building manors and mansions, the gentry will not fell trees” (Coggins 2003:199). The implications of *fengshui* were also sociopolitical and trans-generational. A village history from Anhui warns, “Every family must take care of the mountains and waters around. Plant trees and bamboo as shelters. … Keep an eye on the environment and protect it from damage. This is a chore for people of one hundred generations to undertake” (Coggins 2003:199–200). The practices of *fengshui* have suffered in modern China under the combined pressures of Communism, which disavowed the spiritual realities that *fengshui* addressed, and, more recently, free market capitalism, which has emphasized the preferences of individuals above the good of the community. Today, deforestation rates in China are among the highest in the world (MacBean 2007).

These historical cases from Greece, Israel, and China are among many examples which demonstrate that, whether given a teaching from a scholar, a command from God, or a charge from ancestors, people often neglect and degrade the world around them. Neither Plato’s remembrances of a better landscape, nor religious commands that revealed land as an object of God’s care and concern, nor sacred traditions of ancestors and kin have been sufficient to keep people from selfish behavior that often ruined their environment.

Such case histories, diverse as they are in locality and worldview, reveal common patterns in human interaction with nature. Taken together, they reflect the principle that human interaction with nature is determined primarily by the characteristics of the surrounding environment, the characteristics of the local human economy that obtain needed and desired resources from nature, and human ideas and attitudes about nature (Figure 1.2). In Plato’s example, hilly and mountainous terrain (the state of nature) combined with herding and farming (the human economy) with an assumption that the land exists for growing crops and raising animals (the human attitude toward nature), led to rapid soil erosion and loss of productivity. In the case of ancient Israel, a divine revelation offered a means to change this customary understanding of “the land” (nature) from a commodity to be used to an entity enjoying a “right” to rest. Although the “new” idea was not embraced and obeyed, it provides an objective manifestation of the abstract concept that human attitudes toward nature must regard it with value if human communities are to move from exploitive forms of “management” to meaningful conservation. In China, traditional practices were meant to reflect right relationships between human beings and their physical environment as part of an underlying spiritual goal of harmony and unity in all things. But, in China as elsewhere, this has proved difficult to achieve.

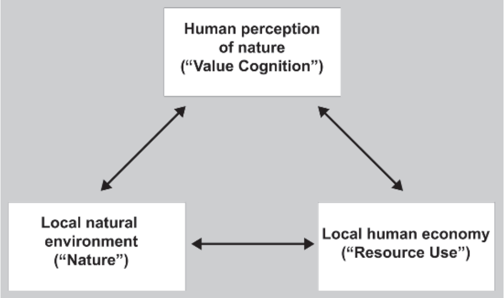

FIGURE 1.2. The “environmental impact triangle” displaying three key elements of human environmental impact on nature: the interaction of the characteristics of the local natural environment (nature), the kind of local human economy employed by the human community, and the perceptions of and attitudes toward nature by humans. Only when human perception begins to view nature as something of value in itself, or something to be sustained beyond immediate need for future generations, does “conservation” emerge as a consistent practice in the human community. (Developed from concepts described by McEvoy (1988).)

Changes in human attitudes toward nature affect human treatment of it. Although humans have “managed” their physical environment for millennia, they began to conserve nature only as they embraced certain ideas about it. One is that non-human creatures, and even the physical landscape itself, possess intrinsic value, that they are “good” in and of themselves. The sources of this perception are varied (Chapter 2), but, whenever humans begin to perceive nature and natural objects as good in their own right, they begin to treat them with greater respect. The perception of intrinsic value leads to considering the interests and needs of the thing valued. When such things are considered as having “a good of their own,” humans begin to consider what would be “good for them.” That is, what human action would produce conditions that would be “good” for nature? When humans begin to embrace this idea, they begin to take actions that are the beginnings of “conservation.”

This kind of thinking is not new. Over a thousand years ago, Graceo-Roman culture, as well as Judeo-Christian and Chinese religious traditions offered rationales for the concept of “Natural Rights,” providing a basis for the belief that natural objects, although not ***moral agents*** (capable of knowing right from wrong) were to be recognized as ***moral subjects*** (capable of being treated by humans in a right or wrong manner). Some kinds of animals, plants, or even "the land," as described in Leviticus 25, were protected by Greek or Roman law or Judeo-Christian religious precept from abuse, cruelty, or inappropriate treatment. Similarly, in China, living creatures were sometimes elevated to the status of participants (as the defendant or the accused) in civil or criminal trials (Coggins 2003:67).

Human societies have always benefited from the use of natural resources, but conservation is initiated when such societies began to think about resource use for future generations. When human societies begin to think of themselves as trans-generational, they also begin to think of how to use resources in a way that is ***environmentally sustainable***. But in order for resource use to be sustained, the natural processes and functions that produced the resource, whether clean water, fertile soil, good crops, timber, or abundant game, must continue to function properly, and therefore must be *conserved* over time.

An example of this kind of thinking can be found in the words of former US President Theodore Roosevelt. Explaining his policy on forest reserves to a joint session of Congress, Roosevelt stated, "It is the cardinal principle of the forest-reserve policy of this Administration that the reserves are for use. Whatever interferes with the use of their resources is to be avoided by every possible means. But these resources must be used in such a way as to make them permanent" (Roosevelt 1926:235).

1.2.3. Conservation as Expression of Privilege

Many early efforts in conservation were not achieved by ethics, but enforced by punishment. In many cultures, conservation began with efforts to preserve nature by prohibiting some or all human use of resources in particular areas, except for a privileged few. European and Asiatic royalty and other wealthy individuals set aside land as hunting and forest preserves, forbidding "common people" to kill game animals, or even gather sticks within preserve boundaries. Violators were imprisoned or even killed for their trespasses. Indeed, the word "forest," a term of European origin, originally referred to areas where nobility had exclusive rights to game and timber, controlling how much was taken and how much remained. William of Normandy established one such reserve, the New Forest, in England in 1085. Regarding his affection for his New Forest and its creatures, one contemporary wrote that "he loved the stags as dearly as though he had been their father" (quoted in Holdgate 1999:2). Perhaps that is why he did not allow anyone to hunt the stags without his permission, and severely punished any who did.

With similar rationale and motivation, Chinese royalty protected some game preserves with walls and guards, and during the Qing Dynasty (1644–1911), even established a government agency called the "Bureau of Imperial Gardens and Hunting Parks" where royal reserves were divided into three categories: (1) Hunting Enclosures, (2) Enclosures for Provision for the Royal Household, and (3) Enclosures for Military Training (Coggins 2003:11). Although such prohibitions were primarily expressions of royal prerogative, they also represented an early recognition of the limits of resource use, namely, that natural resources, such as forests or animal populations, could not produce sufficient resources for exploitation by everyone. Unless such exploitation was limited, the resource would degrade.

In western societies, cultural expressions of conservation advanced from preservation by prohibition to active manipulation and management of natural resources. In Europe, wealthy individuals employed gamekeepers, whose function was to ensure an abundance of favored species for hunting. Gamekeepers accomplished this, in part, by keeping out vagrants and poachers, but also through such activities as killing predators, introducing and translocating game animals to increase their densities, and even manipulating habitat.

Such activities did not achieve a consistent approach to conservation because they operated within established social boundaries of class, rank, and economic status characteristic of feudal societies and aristocracies. Sometimes their long-term effects were exactly the opposite of "conservation." In the United Kingdom, killing game, cutting trees, or even trespassing in royal reserves was a serious offense, and violators often were deported to Australia, which the British originally used as a penal colony. Ironically, this practice helped to create a strong anti-conservation sentiment there. As historian John McCormack noted "the idea of game laws was anathema to many Australians" (McCormick 1989:7). The abundance of Australian fauna suggested that it should be the everyone's right to kill animals without hindrance. Thus, "because Australia was a free and expanding young society, it would reject the notion of conservation of fauna as a hated relic of the feudal past from the Old Country" (McCormick 1989:7).

1.2.4. Conservation as Right Relationship with Nature – The Arcadian Vision

On the island of Peloponnesus, in what is today modern Greece, was the province of Arcadia. According to Greek mythology, Arcadia was the domain of Pan, god of the forest, and his court of dryads, nymphs, and other spirits of nature. Arcadia's renowned beauty, as well as the presence of spiritual beings, gave it a reputation as an earthly paradise. Its human inhabitants were known for their simple, pastoral way of life, living in harmony with nature.

Over time, European art and literature transformed the concept of Arcadia into an idealized place where both people and nature lived in harmonious simplicity, uncorrupted by the vices of civilization, such as is portrayed in William Shakespeare's play, *A Midsummer Night's Dream*, where an Arcadian-like realm is ruled by a fairy king and queen. An excellent example of the Arcadian ideal in literature comes from the English poet William Wordsworth, who wrote many poems extolling the beauty and virtues of nature, and the value of living in harmony with it. We can see this in his poem about a shepherd, Michael, of the Lake District in England who lived and worked among

> *Fields, where with cheerful spirits he had breathed*
> *The common air; hills, which with vigorous step*
> *He had so often climbed; which had impressed*
> *So many incidents upon his mind*
> *Of hardship, skill, or courage; joy or fear;*
> *Which like a book preserved the memory*
> *Of the dumb animals, whom he had saved,*
> *Had fed or sheltered, linking to such acts*
> *The certainty of honorable gain*
> (Wordsworth 1975:63)

Although such an idealized view of nature did not stimulate actions or policies that we would today regard as conservation, it did begin to create the perception that humans and nature were meant to live in harmonious relationship, that nature was to be valued for its own sake, not for consumptive or utilitarian purposes. The Arcadian view of nature provided a foundation for the beginnings of a conservation mentality in western Europe and North America that would eventually grow to express itself in more specific and tangible ways.

1.2.5. Conservation as Knowledge – The Invitation to Study and Appreciate Nature

In 1788, an obscure British clergyman, Gilbert White, pastor of the Church of Saint Mary's in the village of Selborne, England, published his records of over 20 years of natural history study and observation. His book's humble and homely title was *The Natural History and Antiquities of Selborne*. No one then could have foreseen its enormous success and popularity. Two hundred twenty years later White's work remains one of the classics of natural history, continuously in print from the time of its publication, and among the most published books in the English language.

The Natural History and Antiquities of Selborne is, in many ways, simply a very well written and engaging naturalist's journal of his local surroundings. White never ventures far from home, often writes about common and supposedly insignificant creatures, and presumes no scientific credentials, authority, or mandate to justify his work. Yet his careful studies, exact and direct observations, simple but elegant experiments, and pleasant, congenial warmth and humor made significant contributions to science and drew thousands of people, formerly uninterested in nature, into more careful and intentional study of their surrounding world. White, now considered England's first ecologist, grasped the importance of earthworms for soil productivity, was the first to describe the harvest mouse as a species distinct from other kinds of mice, and noted the timing of hibernation in a tortoise. In the last example, one can see an example of White's inimitable style:

> *A land-tortoise, which has been kept for thirty years in a little walled court belonging to the house where I now am visiting, retires under ground about the middle of November, and comes forth again about the middle of April. When it first appears in the spring it discovers very little inclination towards food; but in the height of summer grows voracious: and then as the summer declines its appetite declines; so that for the last six weeks in autumn it hardly eats at all. Milky plants, such as lettuces, dandelions, sow-thistles, are its favourite dish. In a neighbouring village one was kept till by tradition it was supposed to be an hundred years old. An instance of vast longevity in such a poor reptile!*

White's writings offered no specific appeals to "conserve" nature. There was no incentive to do so because White simply wrote about the world as he knew it, one in which there was no scarcity of life in the world of nature and no apparent threat to its continuance. Grounded in the Arcadian view that nature was to be enjoyed for its own sake, and that an attitude of simplicity and humility were the prerequisites for such enjoyment, White's work encouraged ordinary people to "make the acquaintance" of nature, to pay attention to and be careful observers of the non-human world. In his own words, White frames this invitation to the reader in a poem he places at the beginning of his book.

> *See, Selborne spreads her boldest beauties round*
> *The varied valley, and the mountain ground,*
> *Wildly majestic! What is all the pride,*
> *Of flats, with loads of ornaments supplied?*
> *Unpleasing, tasteless, impotent expense,*
> *Compared with Nature's rude magnificence.*
> *Arise, my stranger, to these wild scenes haste;*

As years passed, readers of White, particularly in the United Kingdom began to see the world that White described, studied and loved as increasingly imperiled by the unrestrained expansion of industrial development, and with it the quality of life for people. As a result, one of the first expressions of conservation in England, and later much of western Europe, is often described as the "Back to the Land" movement (Guha 2000:6), a movement that idealized the rural life originally expressed in the Arcadian perspective. White's work, appearing during the early stages of the British industrial revolution, struck an emotional chord with English and other European readers who were beginning to see the darker side of progress apparent in industrial development and attendant pollution. The nineteenth-century English social critic and ethicist John Ruskin described British industrial progress as "the frenzy of avarice … daily drowning our sailors, suffocating our miners, poisoning our children, and blasting the cultivatable surface of England into a treeless waste of ashes" (quoted in Cook and Wedderburn 1908:137). Anthropologist Alan McFarlane noted of conditions during that time, "England was the most industrialized country in the world, yet one where the yearning for the countryside and rural values was most developed. Its strangely anti-urban bias was shown in the prevalence of parks, the ubiquity of flower gardens, the country holiday industry, the dreams of retirement to a honeysuckle cottage …" (McFarlane 1987:77). The nineteenth-century English poet William Morris captured the spirit of this longing for the simple country life and the pleasures of rural nature in his poem, "The Earthly Paradise," which began

Forget six counties overhung with smoke,
Forget the snorting steam and piston stroke,
Forget the spreading of the hideous town;
Think rather of the pack-horse on the down,
And dream of London, small, and white, and clean,
The clear Thames bordered by its gardens green …
(Morris 1905)

White's work was essential in providing a detailed picture of what such a "back to the country" life might be like, and, in doing so, created a cultural climate in England receptive to the first and earliest organized conservation efforts in the western world, including the first organizations formed specifically for conservation purposes. Among these were the Commons Preservation Society, initiated in 1865, that was formed to prevent urban areas from encroaching on natural woodland and heath ecosystems (Guha 2000:16). Three years later in 1868 another conservation organization, the Association for the Protection of Sea Birds (APSB), was formed, and its formation is a story worth telling.

1.2.6. Conservation to Save Species – Origins of the First Conservation Organizations

Following the example of White, many English citizens, including many members of the clergy, became devoted students of natural history. Like White, clergy often were particularly attracted to such study because, understanding the world as a "good" creation of God (Genesis 1), they believed that such study would lead them, and their congregations, to a fuller grasp of God's providential character and goodness toward all that he had made. One individual who exemplified this pattern was the Reverend Francis Orpen Morris (Figure 1.3). Beginning his work of overseeing the church at Nafferton in East Yorkshire, England, in 1844, Morris began to develop a reputation as a naturalist through his books on natural history, especially bird identification. Through such work Morris became acquainted with many of England's best scientists, including John Cordeaux, a prominent naturalist of the time. Cordeaux was particularly interested in the study of bird migration, and naturally focused his investigations on sea birds and shorebirds along the Yorkshire and Dunham coasts. Independently, both Morris and Cordeaux became alarmed at the large numbers of sea birds being killed by unregulated sport hunting, particularly in the spring. At that time bird shooting and egg collecting were widespread and unregulated. By the 1860s, in the 18 miles of coastline between Bridlington and Scarsborough where Morris worked and lived, it was estimated that 120,000 birds were annually trapped or shot between April and August. One man boasted to Morris that he had killed 4,000 gulls in one season.

FIGURE 1.3. Francis Orpen Morris, a British clergyman who was instrumental in founding the world's first organization for species' conservation, the Association for the Protection of Sea Birds. (Courtesy of Ash Midcalf and Birdcheck, http://www.birdcheck.co.uk/)

Alarmed by these events, Morris presented a petition to the House of Commons calling for a heavy tax on guns, a move he hoped would curtail the loss of birds in England, especially the loss of seabirds and shorebirds in coastal areas. Morris engaged the help of his vicar (bishop), the Reverend Henry Frederick Barnes, along with Cordeaux, to find ways to stop the slaughter of sea and shore birds. Barnes, who knew Morris as both a fellow Christian clergyman and bird lover, decided to attack the problem by forming an organization specifically dedicated to sea bird protection. To form such an association, Barnes used his influence to convene a meeting of local clergy and naturalists in 1868 to establish the organization, the Association for the Protection of Sea Birds (APSB). At the same time, Barnes worked to secure the support of local landowners to prevent hunter access to sensitive areas, and then added additional political and social clout by gaining the support of his own superior, the Archbishop of York, as well as that of several members of Parliament. Barnes contacts in Parliament then sponsored a bill, the Sea Birds Preservation Act, which passed parliament in June 1869 and enforced a closed season from 1 April to 1 August. The first successful prosecution under the Act took place in Bridlington on 10 July 1869 when Mr. Tasker, of Sheffield, was fined £3 19s for shooting 28 birds (Dyson 1997).

The formation of the APSB marked the beginning of the establishment of societies to protect specific plants and animals. The formation of the British Royal Society for the Protection of Birds (BRSPB) followed in 1889. In the United States, the BRSPB was preceded by the formation of the American Ornithologists Union in 1883 and the National Audubon Society in 1886. Although the formation of the APSB marked the beginning of species specific conservation efforts through organized conservation advocacy, a second major form of conservation, the creation of parks and nature preserves from existing landscapes, would be radically affected and transformed by developments in the United States, creating a model for land- and ecosystem-based conservation that would come to be imitated throughout the world. This was the concept of the modern National Park.

1.2.7. Conservation as Preservation of Landscape – The Washburn Expedition Goes to Yellowstone

In Europe, centuries of human impact on the natural landscape left few areas unchanged by human presence, and unaffected areas that remained were often small and remote. There was little opportunity to establish large areas for conservation purposes, so reserves set aside for species or habitat protection were small. The first nature reserve, and one still in existence today, was the Karpfstock, a mountain in Switzerland where the Canton (Council) of Glaus forbade hunting by anyone in 1576 (Holdgate 1999:3). At a similar scale, the Dutch Prince William of Orange set aside The Wood of the Hague in 1576. By 1826, the English had established Walton Park as the worlds' first bird sanctuary. But in these and other cases, the areas preserved were small and not unaltered by human habitation or development. In a remote region of the western United States, an 1870 expedition would initiate an entirely new paradigm in conservation at a regional landscape level: the US National Park.

In 1807, John Colter, who left the Lewis and Clark expedition in 1806 to become an independent trapper and explorer, found a region of incredible scenic beauty and unbelievable thermal wonders, including geysers, "pots" of boiling mud, petrified forests, and hot springs in what is today northwestern Wyoming. His reports of the area were not initially believed, but led others to name the area "Colter's Hell." A mountain man and military scout, Jim Bridger, explored the area 23 years later in 1830. He returned with even more incredible stories, including tales of a river fed by geysers and thermal springs that "got hot on the bottom" (what is called today the Firehole River), cliffs of black glass (obsidian), and springs belching sulfurous steam. But his reports, sometimes embellished (Bridger spoke facetiously of "petrified birds that sing petrified songs in petrified trees" in the Yellowstone country) were also treated with doubt, and often referred to as "Jim Bridger's lies" (Frome 1987).

Despite public skepticism, persistent rumors of the region's incredible natural wonders eventually led to a number of visits to the area by other explorers and early settlers, and their reports continued to build its reputation. Finally, in August of 1870, an official expedition led by the Surveyor General of Montana, Henry Washburn, with US Army Lieutenant Gustavus Doane commanding a military escort, left Fort Ellis, Montana and proceeded toward "Colter's Hell." The Yellowstone River and its surrounding area, the "Yellowstone Country," were so called because of the yellow- and copper-colored formations of rhyolite, a volcanic rock, that characterized the river's deep and spectacular canyons (Clepper 1966; Frome 1987). At their first night's camp, the expedition members posted a watch in order to, in the words of one, "keep the Indians from breaking the eighth commandment," (Anonymous 1871). Despite their fears, the expedition members enjoyed themselves immensely. Speaking of the trout they caught, one wrote, "Few of them weighed less than two pounds, and many of them over three. They had not been educated up to the fly, but when their attention was respectfully solicited to a transfixed grasshopper, they seldom failed to respond" (Anonymous 1871).

The members of the Washburn expedition found the area even more amazing than the earlier tales they had heard and meticulously chronicled and sketched what they encountered. One member, Cornelius Hedges, described a thermal spring they observed near one camp in a meadow. "This spring, with two others, was situated in about an east and west line, and at the upper side of the basin, which opened south, toward the creek. The central one of these three was the largest of all, and was in constant, violent agitation, like a seething caldron over a fiery furnace." (Anonymous 1871). Speaking further of these and similar springs, Hedges remarked, "It is said that Indians do not go above the grand *canon* on the Yellowstone. Whether this is true I know not, but I imagine the unscientific savage finds little to interest him in such places. I should rather suppose he would give them a wide berth, believing them to be sacred to Satan. If a person should be cast into one of these springs, he would be literally immersed in a lake of burning brimstone" (Anonymous 1871).

Seated around the flames of a campfire on a September evening at the junction of the Firehole and Gibbon Rivers, the members discussed the remarkable wonders of the area and what ought to be done about them. Hedges suggested that they should not abandon the area to commercial development. Rather, Yellowstone should be set aside as a "national park" for the enjoyment of US citizens, as well as visitors from around the world (Frome 1987). It was an idea never before proposed, that a government should preserve the best part of its natural heritage so as to make that heritage accessible to everyone, a uniquely democratic vision of conservation. What US historian and environmental novelist Wallace Stegner called "the best idea we ever had" (Stegner 1998:137) rose from the sparks of an evening campfire to become an ideal emulated round the world – the ideal of the national park.

Convinced of the rightness of their vision, leading members of the expedition returned to the East to initiate a campaign for Yellowstone's preservation as a national park. A scientific expedition the following year confirmed their reports, complemented by the stunning photographs of William Henry Jackson and the dazzling paintings of Thomas Moran (Figure 1.4), both of whom accompanied the expedition. On March 1, 1872, Congress approved a bill creating Yellowstone National Park "as a public or pleasuring ground for the enjoyment of the people" (Petulla 1977). By 1916, Congress would create the National Park Service, directing it to "conserve the scenery and the natural and historic objects and the wild life therein, and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations" (National Park Service Organic Act 1916) Today, much of the worldwide effort in conservation biology rest on the legitimacy of designing and establishing conservation reserves, and on the assumption that such reserves are an important part of national and cultural heritage. Such a foundational premise of conservation is now so familiar that it is taken for granted. In truth, the idea of landscape scale conservation reserves, first expressed in the US concept of the National Park, is a radical and recent concept. It created an enduring paradigm for conservation throughout the world, and was widely exported as a model for other countries. The ***Yellowstone Model***, however, was strongly influenced by North American landscape characteristics, as well as by perspectives and prejudices of US culture.

FIGURE 1.4. Castle Geyser, Upper Geyser Basin, Yellowstone National Park, painted by Thomas Moran, official artist of the 1871 US Geological Survey Expedition to Yellowstone. (Courtesy of US National Park Service.)

The expedition members were primarily concerned with the enjoyment of their fellow citizens, not with the preservation of the Yellowstone Ecosystem. They envisioned a form of "development", facilitated by the railroad, that would make Yellowstone accessible to millions with relatively little cost or effort. One member expressed these aspirations this way.

> *As an agricultural country, I was not favorably impressed with the great Yellowstone Basin, but its brimstone resources are ample for all the matchmakers in the world. A snow-storm in September, two feet deep, is hardly conducive to any kind of agriculture or stock-raising; … When, however, by means of the Northern Pacific Railroad, the falls of the Yellowstone and the geyser basin are rendered easy of access, probably no portion of America will be more popular as a watering place or summer resort than that which we had the pleasure of viewing….*
>
> (Anonymous 1871)

And, as implicit in Hedges' words about the "unscientific savage," there was no consideration as to how the Park's establishment would affect the native Americans that were living in it.

Modern conservationists may be forgiven for smiling at the thought of seeing Yellowstone National Park as a giant supply depot for match making, but it is well to remember that even well-educated people seldom challenge the cultural patterns of thinking in which they have been raised and educated. The US would not expressly establish a national park to protect an "ecosystem" until the formation of the Florida Everglades National Park in 1934. With all its cultural blind spots, the US vision of the national park was a watershed event in the development of conservation biology, for it formalized the concept of setting aside land areas of landscape scale specifically to preserve natural settings, and the animals and plants within them. Following the creation of Yellowstone, the US concept of the "National Park" began to be imitated throughout the world, with Australia establishing its first park in 1879, Canada in 1885, Africa (several countries) in 1890, and Sweden in 1903. This model of nature preservation, while noble in its emphasis on access and enjoyment for all persons, regardless of station, nevertheless reflected the US experience of having large, relatively uninhabited areas of land available for such protection. In much of the world, this was not the case, and new models of national parks and nature reserves would be needed for conservation goals to succeed. We will return to this problem as we follow the development of conservation in different parts of the world. But first we explore the origins and implications of the "Yellowstone Model" to better understand its global influence.

POINTS OF ENGAGEMENT – QUESTION 1

How might the history of conservation in the United States, and perhaps the world, have been different if the members of the Washburn Expedition had seen the Yellowstone region as an opportunity for personal financial gain and private entrepreneurship?

1.3. Intellectual Foundations and History of Conservation in the United States

1.3.1. Conservation as Moral Mission – John Muir and Theodore Roosevelt

The American conservationist, John Muir (Figure 1.5), although generally credited as the person most responsible for the development of the US National Park Service and System, spent most of his years as a conservation activist concerned with the practical problem of how to save the Sierra Nevada Mountains of California from logging, mining, hydrological development, and other forms of commercial exploitation in the late nineteenth and early twentieth century. Prior to his work in conservation, Muir invented and manufactured mechanical equipment, but nearly lost his eyesight in an Indianapolis carriage factory when a file he was using slipped and went through one eye. Eventually recovering his sight but shaken by this near life-altering experience, he retired to the wilderness in an attitude of repentance and reexamination of his life. After traveling on foot for over a thousand miles through parts of Florida, Georgia, Kentucky, and Tennessee, he eventually reached the Sierras. There, Muir had an intense religious experience, gaining a sense of profound fulfillment and exaltation, as well as an intense oneness with the land around him (Petulla 1977). But, seeing destruction and degradation of the Sierras and other natural areas everywhere, Muir at once began a public campaign to save the American wilderness.

Muir was an eloquent and persuasive writer, and his articles in major newspapers and national magazines urged Americans to (temporarily) leave the cities and enjoy the wilderness. As his experience had been religious, his writing unapologetically used religious language to express his concerns, as exemplified by the title of one of his early and most influential articles in the Sacramento (California) *Record-Union* titled, "God's First Temples: How Shall We Preserve Our Forests?" (Petulla 1977). His worldview, as well as his combative nature, his moral absolutism in conservation, and his attitude toward the "development" of his beloved Sierras, are best understood in his own words. In one example, written after the establishment of Yosemite but still in the heat of the conflict over the use of the Sierras, Muir wrote

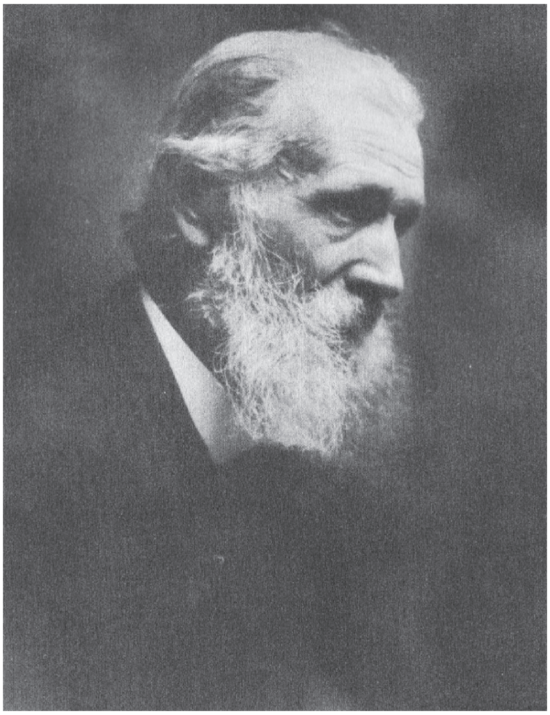

FIGURE 1.5. US conservation activist John Muir, founder of the Sierra Club and champion of the Preservationist Approach to conservation. Muir, who framed conservation as a question of moral choice, was instrumental in establishing the US National Park Service. (Photo courtesy of Dan Anderson.)

> *The battle we have fought, and are still fighting, for the forests is part of the eternal conflict between right and wrong, and we cannot expect to see the end of it.... The smallest forest reserve, and the first I ever heard of, was in the Garden of Eden; and though its boundaries were drawn by the Lord, and embraced only one tree, yet even so moderate a reserve as this was attacked. And I doubt not, if only one of our grand trees on the Sierra were reserved as an example and type of all that is most noble and glorious in mountain trees, it would not be long before you would find a lumberman and a lawyer at the foot of it, eagerly proving by every law terrestrial and celestial that the tree must come down. So we must count on watching and striving for these trees, and should always be glad to find anything so surely good and noble to strive for.*
>
> (Muir 1896:276)

Muir was the father of a new school of thought and activism in US conservation, the philosophy of preservationism. Muir and other preservationists condemned the

Figure 1.6. Henry David Thoreau, whose writings on simplicity and personal connection with the land spurred interest in conservation in the US in the late nineteenth and twentieth centuries. (Photo courtesy of US Library of Congress.)

destruction of nature to satisfy what he considered the greedy appetite of materialism. Earlier American writers like Ralph Waldo Emerson and Henry David Thoreau (Figure 1.6) had refined the Arcadian Ideal into the more formal philosophy of ***Romantic Transcendentalism***, a view that argued that the highest and best use of nature was not the extraction of its resources as commodities for human use and material goals, but the appreciation of its intrinsic values and aesthetic qualities through which the human spirit was transformed, a place where one could draw near to and commune with God (Callicott 1990). Muir shared this view, and made it clear in his writings that people who used nature as a place for religious worship, aesthetic contemplation, inner healing, rest, and relaxation were making a "better" (that is, morally superior) use of nature than those who cut trees, dammed rivers, mined minerals, or plowed the soil. Nature, Muir believed, was to be preserved in an undisturbed state so that the higher uses and values could be appreciated and enjoyed. And Muir went further. As he worked out the practical implications of the transcendentalist' view, Muir became a fierce advocate of protecting nature from development and exploitation precisely so that it could be enjoyed in these higher and better ways. Muir was instrumental in framing the debate in conservation around the essential question: What is the best use of nature and natural resources? This question is still at the core of the conservation debate and remains a key to understanding the development of conservation biology as a scientific discipline and a cultural force.

1.3.2. "Scientific Conservation" Through Sustained Yield – Moral Mission Gives Way to Utilitarian Purpose

1.3.2.1. The Federal Government Empowers Conservation as Science and Democratic Ideal

Even as Muir was framing the key question of the great conservation debate as a moral appeal, the end of the western frontier in the United States also began to affect a profound change in American environmental attitudes. Settlers had been faced with a hostile, often life-threatening environment on the frontier that could be made livable only by strenuous individual effort and significant environmental alteration. Yet, for all its hardship, westward expansion gave a continuing impression that there would always be new lands to settle and more natural resources to find and use. The passage of the Homestead Act of 1862, which offered a free 160 acres (65 ha) of western land to any person who would build a house on the acreage and live in it for 5 years, provided motivation for thousands of US citizens, especially those without land of their own, to begin dreaming of a new life in the West. The end of the US Civil War in 1865 brought peace to the nation, released most men from military service, and thus reunited hundreds of thousands of families throughout the country, brought the opportunity for people to begin making plans for westward movement. And the completion of the transcontinental railroad in 1869 gave ordinary citizens a means of transport to western areas formerly inaccessible to them. Armed with such means, motive, and opportunity, US citizens began to move to and occupy formerly remote western areas. As the frontier came to an end and the density of human populations in the US began to grow even in remote areas, US citizens now found themselves living in a nation of increasingly well-defined physical and environmental limits. At the same time, use and exploitation of natural resources began to shift from individual to corporate effort, and from simple exertions of human and animal labor to increasingly sophisticated applications of advanced technologies. Freed from many of the former limitations, corporate interests in mining, lumber, fishing, and grazing began to exploit and alter resources rapidly over large areas. For example, the state of Michigan, the nation's largest producer of timber as recently as 1900, had removed most of its commercially valuable timber by 1920, and effectively cut itself out of the lumber business (Dickman and Leefers 2003). In states further west, similar trends were in motion.

The establishment of Yellowstone as a US national park had set a legal and political precedent for the US federal government to take a more active role in conservation, but the exact nature of that role remained undefined. As the role of the federal government in conservation began to grow, it began to take two separate, sometimes conflicting, paths in conservation. One led to an increasing role in establishing parks and nature preserves that were to be protected from exploitation and disturbance because of their own intrinsic value, the other to the increasing management and administration of lands on which resources would be used and harvested sustainably for the public good.

The establishment of Yellowstone Park was a monumental step for the federal government down the first path, but pursuit of the second began at almost the same time. In 1873, just 1 year after establishing Yellowstone, the US Congress, in an effort to aid western homesteaders, passed the Timber Culture Act, which permitted the clearing of up to 160 acres of timber if the owner replanted trees on 40 of those acres. Although intended to help individual families, the law was used most effectively by timber companies to clear large tracts of forests with minimal reforestation. In 1891, at the urging of many scientific and professional societies, President Benjamin Harrison, aided by his Secretary of the Interior, John W. Noble, succeeded in persuading Congress to pass a bill repealing the Timber Culture Act and granting (in a relatively unnoticed rider on the bill) the president authority to set aside forest reservations (Petulla 1977). The Forest Preservation Act, as it came to be called, was designed to further protect American forests from suffering the same fate as their counterparts in the states of Michigan, Minnesota, and Wisconsin.

As many private citizens were becoming increasingly vocal in their opposition to the consumptive use of natural resources, particularly on public (federal) lands, the power of the federal government and its involvement in conservation was growing. The assassination of President William McKinley in 1901 brought his young Vice-President, Theodore Roosevelt, to the Oval Office (Figure 1.7). Roosevelt, an active outdoorsman, began to take an interest in western lands, particularly in the use of forest and wildlife resources. By this time John Muir, an ardent preservationist, had formed the Sierra Club, whose expressed purpose was "to enlist the support of the people and the government in preserving the forests and other features of the Sierra Nevada Mountains" (Petulla 1977). In his campaign to save the Sierras, especially Yosemite Valley, Muir convinced the US federal government and the California legislature to make Yosemite, then a state preserve, into a national park. Muir's influence, empowered by Roosevelt's position and actions as President, gained acceptance for the concept of national parks throughout the West and laid the foundation for the eventual establishment of a government agency, the US National Park Service, to oversee their management. Roosevelt continued to express a preservationist philosophy of conservation through the development of a national wildlife refuge system, one that would become a model for countries throughout the world. With the establishment of Pelican Island, Florida, as a wildlife sanctuary in 1902, Roosevelt began an ambitious program to create federally protected wildlife sanctuaries throughout the US, establishing 52 such sanctuaries during his administration, along with 16 national monuments and five national parks. The refuges Roosevelt preserved were the beginning of what would grow to become the National Wildlife Refuge System of the US Fish and Wildlife Service (USFWS), although the USFWS itself would not exist as a federal agency until many years later.

FIGURE 1.7. Theodore Roosevelt, the US President who made conservation a national priority during his presidency from 1901 to 1909. (Rockwood Photo Company 1903. Courtesy of US Library of Congress.)

Ironically, the pursuit of the second pathway of government involvement in conservation, one that led to increasing management of the sustainable use and harvest of natural resources, also was furthered under Roosevelt, aided by his association with John Muir. Alerted and persuaded by Muir and others of increasing environmental degradation in the American West, Roosevelt increasingly viewed the large corporations that were unfairly profiting from western lands with hostility and distrust. Known as "The Trustbuster" before the end of his first administration for his zeal in breaking up industrial monopolies in the East, Roosevelt came to view the corporate practices of logging and mining in the West with similar hostility, not only wasteful but undemocratic. To Roosevelt, it was clear that a handful of individuals and their companies were reaping most of the profits from natural resources that rightfully belonged to all citizens, so he increasingly saw federal regulation as both appropriate and necessary because he viewed the federal government as the only institution powerful enough to oppose these corporate timber and mining interests that threatened to destroy the landscape.

On this basis, Roosevelt used the provisions of the Forest Preservation Act aggressively and often by setting aside large forested areas in the western states. Although the administration of such lands was logically the domain of the Department of the Interior, Roosevelt distrusted that agency, fearing that corporate interests in timber and mining corrupted it. Determined to protect the new forest reserves, Roosevelt created a new federal agency, the US Forest Service. He placed it in a department he considered less corrupt – the Department of Agriculture – and put his own man, Gifford Pinchot, in charge of it (Figure 1.8). But this appointment brought conservation efforts in the United States under the influence of conservation practices developed much earlier in European settings.

1.3.2.2. German Influences in Conservation – Forest Monocultures and Maximum Yields

In Europe, with its longer history of human settlement and landscape cultivation, natural resources like forests were managed by human manipulations in ways that were not fundamentally different from those of commercial agriculture. The most advanced techniques were practiced by Germans, who essentially founded the disciplines of silviculture (tree growing) and forest management in the eighteenth and nineteenth centuries. Under a strong central government during the reign of Fredrick the Great of Prussia (1740–1786) that practiced close supervision of state forests, German foresters began to move from traditional "area-based" concepts of management, that focused on dividing forest units by landscape features, to a "yield-based" management approach. The yield-based management system, which worked best with stands containing only a single species, was based on direct estimates of volume and weights of trees of different ages. By studying growth patterns that could be determined on small, experimental plots, German foresters were able to develop highly accurate and predictive standard yield tables for every species of commercially important tree. Using such tables, foresters could accurately estimate not only the wood mass of individual trees but of entire stands, even over fairly long time periods. Armed with such predictive power, German foresters began to develop the concept of ***sustained yield forestry*** which sought to manage the forest in such a way that the same harvest could be reliably removed every year without loss or interruption of forest productivity, an approach that worked best using a "forest plantation" approach to timber management that emphasized single-species systems for maximum timber production.

FIGURE 1.8. Gifford Pinchot, American forest scientist and administrator who developed the US Forest Service and its philosophy of Sustained Yield and Multiple Use during the administrations of US President Theodore Roosevelt. (Photo by Francis Benjamin Johnson between 1890 and 1910. Courtesy of US Library of Congress.)

Encouraged by their successes, German scientists enthusiastically promoted their approaches to forest management abroad, not only in Europe but in its colonies and in the United States and Canada. So esteemed were the German forest scientists of that time that even countries with respected scientific communities of their own often "imported" German foresters for forest management, consultation and practice. In British-dominated India, the first Conservator of Forests was appointed in Bombay in 1847, and another in Madras in 1856, both British citizens. However, by 1864, when the British sought to consolidate their forest management in India under one administrative unit, they appointed a German, Dietrich Brandis, as the first Forest Superintendent of India, empowering his work a year later with the passage of the Indian Forest Act. Brandis organized all Indian forest management under a single administrative unit, the Forest Department of India, and applied German silviculture philosophies and methods to forest management throughout the subcontinent. He would lead the agency for almost 20 years, during which time it would come to control nearly one-fifth of India's land area (Guha 2000:26). Thus, even as the British were imposing "colonial conservation" on India, they were themselves subservient to German concepts of forest management. The German approaches eventually would be challenged, on both scientific and ethical grounds, in the US and also throughout the developing nations of Africa and Asia, but they effectively ruled global conservation practice for much of the nineteenth century and the first half of the twentieth.

The sustained yield forestry developed by the Germans was a classic example, but only one example, of an overall practice and philosophy of conservation marked by a worldwide turning to science and technique-oriented management, an influence that was keenly felt and exemplified in the development of conservation in the United States. In 1886, the US Government made its first appointment of a scientifically trained forester to serve in government-directed forest management. The position was that of Chief Forester of the US Department of Agriculture, and the appointee was not a US citizen, but, again, a German forester, Bernard Fernow. Fernow believed that commercial production of timber was the primary purpose of a forest, and referred to forests as part of the "great economy of nature." His views would set the course of forest management and conservation in the United States for years to come, and indirectly contribute to a serious split in the ranks of the US conservation movement.

1.3.2.3. The Rise of the Resource Conservation Ethic

Within the US Department of Agriculture, an energetic and talented young forest scientist, Gifford Pinchot, rose rapidly to prominence in developing forest management and policy. Pinchot was a US born scientist, but had been trained in German traditions of scientific forest management under the mentorship of none other than Dietrich Brandis. Pinchot also was a younger contemporary, and, for a time, close friend of John Muir, though he was not a preservationist like Muir and did not subscribe to the Romantic-Transcendentalist ethic of nature preservation for the sake of moral values. He saw the timber in the new reserves as an exploitable resource, to be used with careful application of scientific management. Pinchot, in the United States, as well as Brandis in India, saw that high rates of deforestation led to soil erosion, loss of soil productivity, water pollution, and even changes in local climate such as desiccation and drought. Muir believed that such environmental degradation was best stopped by preserving the land from exploitive use, but Pinchot and Brandis saw the solution in scientific forest management. As a result, Pinchot can justifiably be called the father of a new ethic, the ***Resource Conservation Ethic***, sometimes simply referred to as "resourcism" – a view distinct from the Romantic-Transcendentalist Ethic. Pinchot crystallized the philosophy of the movement in a simple, memorable slogan (which he credited to a contemporary, W. J. McGee): "the greatest good for the greatest number for the longest time" (Callicott 1990).

The Resource Conservation Ethic rested on two intellectual pillars. The first was equity – resources should be justly and fairly distributed among present and future generations. The second was efficiency – resources should not be used wastefully. Pinchot and others who advocated a resource conservation ethic were not, like Muir, concerned about the "best" use of nature (which they called "natural resources") in the sense of moral superiority. They were concerned about the "fair" (i.e., democratic) and "sustainable" use of nature. They believed that all interests in resource use, both consumptive and non-consumptive, should be considered and, when possible, satisfied. Time and again Pinchot made clear that, in his view, conservation did not mean protecting or preserving nature. Rather, it meant wise and efficient use of natural resources, informed by scientific study and practice, with the goal of controlling nature to meet human needs over the long term (Nash 1989). This view ultimately led to an end of the friendship between Muir and Pinchot, but neither man wavered in his convictions. Pinchot's view of nature as primarily a source of natural resources to be used productively for the common good led him and others to advance the concepts of ***multiple use*** (using the same systems to supply or satisfy many different needs) and ***maximum sustained yield*** (maintaining a constant level of extractive use approximately equal to the rate of renewal of a renewable resource, such as timber). After his career in the Forest Service had ended, Pinchot helped to establish the Yale School of Forestry at Yale University, the first school of its kind in North America, and one deeply embedded in German philosophies and techniques of forest management for maximum sustainable yield. Although sustained yield and multiple use concepts were being developed and practiced in other parts of the world, they were, in the early twentieth century, nowhere more clearly manifested in land management policies than in the United States. Both were to become important planks in the foundation of modern forestry and became models for other nations in their development of national forest management programs. By the early twentieth century, the rise of independent nation states throughout the world, combined with the growing centralized power of the national governments and the development of ecology as a scientific discipline, permitted the management of lands at national scales. It began to make sense to speak of "national forests" and "national grasslands," among others, as resources managed by a national government for the good of its citizens (Guha 2000:27), and to manage such lands according to strategies of "multiple use" and "sustained yield."

Even as the US federal government was intensifying the extraction and use of resources on public lands for utilitarian purposes, and at the same time establishing an increasing number of national parks and wildlife refuges, another important paradigm in conservation was beginning to emerge in the United States that would influence conservation worldwide. This was the concept of the Wilderness Ideal.

1.3.2.4. Aldo Leopold and the Formation of the "Wilderness Ideal" in Conservation

With an incredible depth of vision, Lieutenaut Gustavus Doane, leader of the military escort of the Washburn Expedition, remarked after his return that Yellowstone should not be viewed simply as a public pleasuring ground, but "as a field for scientific research it promises great results.… It is probably the greatest laboratory that nature furnishes on the surface of the globe" (Holdgate 1999:6). Had Doane been a man of science, he might have had opportunity to act on this remarkable insight and begun unique and original investigations in Yellowstone or other wilderness areas. Instead, it remained for a future scientist of the twentieth century to begin to articulate the value of wilderness in conservation for both scientific and cultural purposes.

Aldo Leopold (Figure 1.9), born and raised in Iowa in the 1880s when that state still had many characteristics of a wilderness, was the son of highly educated German immigrants, and trained as a forester in the best German traditions at Yale University. After graduation, Leopold joined the US Forest Service where he rose with stunning rapidity through the ranks, gaining the position of Supervisor of the Carson National Forest in New Mexico by the age of 24. Along with his obvious intellect and energy, both colleagues and supervisors noticed that Leopold displayed even keener interest and insight toward wildlife than he did toward trees, an orientation not unnoticed by his superiors. Increasingly stimulated by opportunity and encouragement to conduct investigations of game populations in national forests, Leopold, as result of his ongoing studies, became convinced that, like forest management, the practice of game management could be performed scientifically.

FIGURE 1.9. Aldo Leopold, US conservationist and founder of The Wilderness Society, a chief intellectual architect of the "Wilderness Ideal" in conservation at his "shack" near Baraboo, Wisconsin (USA), where he wrote much of his classic work on land ethics, A Sand County Almanac (Chapter 2). (Photo courtesy of the Aldo Leopold Foundation Archives.)

Leopold's experiences and reflections culminated in the classic textbook, *Game Management*, published in 1932, which in turn led the University of Wisconsin at Madison to offer him a faculty position in the field he had created. Leopold accepted the offer and helped to organize one of the first academic departments in wildlife management and wildlife ecology at a state university in the United States.

The synthesis of Leopold's experience in the Forest Service and his studies in academia left him disillusioned with the German models and concepts of intensively managed monocultures as the ideal form of forest conservation. In later years, following a trip to Germany and an inspection of its forests and forestry management practices, Leopold, dismayed by the German obsession with spruce, lamented, “never before or since have the forests of a whole nation been converted into a new species within a single generation.” The Germans, Leopold wrote to a colleague in disgust, had “taught the world to plant trees like cabbages” (quoted in Guha 2000:55). Leopold was not only disillusioned with German-inspired principles of forest monocultures, but also with the philosophical underpinnings of the Resource Conservation Ethic that supported it. Leopold became convinced that such an ethic was inadequate, principally because it was untrue. The land was not, as established management science taught, a collection of separate, compartmentalized entities that could be managed for commodity production. Rather, the land was a *system* of interdependent *processes*, and the outcome of those processes, when they functioned properly, was sustained production of the commodities associated with the processes, such as soil, water, timber, wildlife, and forage for wild and domestic animals. This vision of managing land as a system rather than as a storehouse of commodities led to profound ethical implications about land management and treatment, implications that Leopold would articulate in later years in his most well known book, *A Sand County Almanac*, a work that would ultimately inspire a new ethical philosophy in conservation that would become known as ecocentrism, a philosophy we will examine in detail in Chapter 2: Values and Ethics in Conservation.

Shortly after his appointment at the University of Wisconsin, in 1935, Leopold helped to form The Wilderness Society, a group of scientists, scholars, and conservation activists of varying backgrounds who shared a common conviction that remaining roadless areas, still relatively untouched by mining, industry, logging, and roads, had value if preserved in their current state. Leopold’s claim that “Wilderness is the raw material out of which man has hammered the artifact called civilization” (Leopold 1966:264) reflected a long-held conviction. In 1924, he had been instrumental in getting the US Forest Service to establish its first wilderness area, the Gila Wilderness, in New Mexico. In this way, Leopold led the US in making yet another substantive contribution to global conservation practice, the manifestation of the ***wilderness ideal*** as an important means of conserving landscapes, habitats, and biodiversity, ultimately culminating, after his death, in the passage of the US Wilderness Act of 1964, a law which created the means to develop and administer an entire system of roadless, uninhabited areas, and, in the Act’s own words, “untrammeled by man” and “for the permanent good of the whole people” (Public Law 88–577).

The “Yellowstone Model” of the national park, the “maximum sustainable yield” approach to resource management on public lands, and the “Wilderness Ideal” were not all entirely US inventions, but they were concepts that flourished in US culture, and subsequently exported and adapted throughout the world. However, as a wider world conservation movement began to take shape in the twentieth century, the flaws in such models emerged when they were uncritically accepted and applied in other contexts. As conservation became a global concern and conservationists a global community, new models emerged to make conservation viable in contexts vastly different from the US and European experience.

1.4. The Emergence of Global Conservation – Shared Interests Lead to Cooperation

1.4.1. Multilateral Treaties – The Beginnings of International Conservation Efforts

1.4.1.1. Conservation Driven by Shared Commercial Interests

Even as new forms of conservation in philosophy and practice were emerging in the United States in the late nineteenth and early twentieth centuries, international paradigms of conservation were developing throughout the world. As international commerce and trade increased in the nineteenth century, particularly in the West, and nations found increased cooperation a necessity in international dealings, international agreements and conventions (treaties) began to evolve. Such conventions often addressed resources that could be disputed, “natural” or not, and often governed the use of natural resources, especially migratory animal species, that crossed international boundaries. One of the earliest of these kinds of agreements was the Convention Respecting Fisheries, Boundary, and the Restoration of Slaves established between the United States and Great Britain in 1818. Although this agreement had some indirect effect of protecting some commercial fish stocks, its primary purpose was to provide clear allocation of boundary and property rights between the two nations. Subsequent agreements between Britain and France on fisheries (1867), between European nations on salmon fishing in the Rhine River (1886), and between the US and Britain on the taking of fur seals in the Bering Sea were all conventions driven by the same purpose. Multilateral and bilateral treaties addressing migratory species date to the late nineteenth century (Holdgate 1999).

Initially, international cooperation was motivated by concerns over trade, and the dawning awareness that commerce that depended on migratory species needed those species to have sustainable populations and sustainable levels of harvest. The Treaty Concerning the Regulation of Salmon Fishery in the Rhine River Basin, signed in 1885 by the Federal Republic of Germany, Switzerland, and The Netherlands, prohibited the use of fishing methods that blocked more than half of a watercourse, prescribed specifications for fishing nets, provided for closed seasons and regulation of fishing hours, and promoted captive-breeding. These were all measures designed to enhance the sustainability of the salmon population by reducing its harvest, removing impediments to migration and spawning, and enhancing wild populations by supplementing their numbers with captive ones.

1.4.1.2. International Protection of Migratory Species

One of the oldest problems of conservation is that of managing species that cross national boundaries. Several early treaties addressed conservation of migratory species, including those that bred on the shore or in rivers leading to the ocean, but that spend all or most of their adult life in the sea; migratory marine species that travel over ocean areas across national boundaries; terrestrial species that migrate from breeding to non-breeding areas across international boundaries; and relatively sedentary terrestrial species that live near international boundaries and routinely cross them in the course of normal movements.

From treaties that were concerned with commerce and trade, agreements began to develop that recognized more intrinsic values of the species themselves. In 1902, the International Convention for the Preservation of Useful Birds was signed by 12 European nations. Although it did not protect all species of birds (for example, birds that ate crop plants were not considered "useful," and therefore not protected), it was an important first step in international conservation of migratory species. One of the most effective and enduring treaties protecting migratory birds followed soon after: the Convention between the United States and Great Britain for the Protection of Migratory Birds (1916) which protected birds flying between the US and Canada. Originally motivated by a desire to conserve waterfowl, the treaty established hunting regulations and closed seasons for ducks and geese. It also prohibited hunting of migratory "insectivorous" birds (most songbirds), and established refuges for selected species (Holdgate 1999). A legislative consequence of the treaty was the Migratory Bird Treaty Act (MBTA), ratified in the United States in 1918. The Act prohibited taking or killing of migratory birds without a permit and imposed strict penalties and liabilities for violations. Indirectly, the MBTA was the forerunner of many future US laws that empowered state and federal agencies to regulate hunting and punish violators of game laws, and many of these eventually came to serve as models for other nations.

As the US federal government began to take an increasing role in conservation during the late nineteenth century, it also began to act to secure international provisions for conservation, particularly where such provisions affected US concerns. Given its worldwide interests, influence, and ambitions, the US also took initiative in creating international organizations designed to influence, if not govern, many aspects of conservation policy, such as the International Association of Game, Fish, and Conservation Commissioners in 1902 and the American Committee for International Wildlife Protection in 1930.

Many of these US efforts took place during the administration of Theodore Roosevelt, who viewed conservation as a moral ideal. "There can be no greater issue," he stated, "than that of conservation in this country. Conservation is a great moral issue, for it involves the patriotic duty of insuring the safety and continuance of the nation.... [I] do not intend that our natural resources shall be exploited by the few against the interests of the many, nor do [I] intend to turn them over to any man who will wastefully use them by destruction, ... the rights of the public to the natural resources outweigh private rights and must be given its first consideration" (quoted in Holdgate 1999:8).

Had Roosevelt remained in office, it is likely he would have moved his national concerns for conservation to the international level, and made the United States a leader in international conservation. However, having taken a public pledge not to seek at third term as President, he resigned from office at the end of his second administration. That resignation, the departure of Gifford Pinchot from the Forest Service in 1910, the death of John Muir in 1914, and the onset of World War I sent conservation to the shadows of international politics, although it continued to develop nationally as an issue in many countries.

Leaders of modern nations in the twentieth century increasingly perceived that international cooperation would be the only sure way to achieve international results, in conservation or anything else. The realization of need for increasing international cooperation to protect migratory species from over-exploitation began to be replaced in importance by the emerging awareness of the need for sustainability for future generations. Motivated by a growing level of accountability to their citizens, government officials in democratic countries began to realize that they must act in the best interests of not only the present generation, but of the generations to come. Such realization was an early, emergent perception of the modern concept of sustainability, but, for the first half of the twentieth century, there was no place to even discuss such a concept, let alone promote it through international agreement. A permanent forum for international cooperation had to be established if conservation was to become an internationally coordinated effort, rooted in recognized international law.

1.4.2. Forums for International Conservation – The United Nations and the International Union for the Conservation of Nature

Although nations increasingly began entering into bilateral and multilateral agreements throughout the first half of the twentieth century, there was no recognized international body that could propose or create international laws or treaties aimed at conservation, nor was there any established international organization that served to connect the varied and diverse efforts of conservation beginning to arise in all parts of the world. Some European nations, such as Great Britain, had, in the past, been able to create organizations, laws, and policies of international effect because their influence and jurisdiction applied to all British colonies around the world. Organizations such as The Society for the Preservation of Wild Fauna and Flora of the Empire (1903), while thoroughly "British," affected species protection in Africa, Asia, and South America. However, as colonial domination by European powers declined, there was increasing need for a more representative international body to address global conservation law and policy. It was a scientist and political activist of Switzerland, Paul Sarasin, who first conceived of an international organization whose task would be to attempt to coordinate and unite the efforts of conservation organizations worldwide.

In 1909, Paul Sarasin (Figure 1.10), with his cousin Fritz, founded the Swiss League for the Protection of Nature (or, in its original language, Ligue Suisse pour la Protection de la Nature). An active and respected zoologist, Sarasin urged the Congress of Zoology in the following year to establish "a Committee charged to establish an international or world Commission for the protection of nature … throughout the world, from the North Pole to the South Pole, and covering both continents and seas" (Holdgate 1999:11).

The Congress did establish an *ad hoc* committee, but such a grand scheme as Sarasin's needed more than committee meetings to succeed. Persistent and determined, Sarasin eventually was able to bring together representatives from 16 European nations and the US at a meeting in Berne, Switzerland in 1913. There the representatives agreed to establish a Consultative Commission for the International Protection of Nature, that would assemble and publish issues on the state of world conservation. Unfortunately, the Commission gradually slipped into lethargy and inaction, and finally fell apart. Sarasin did not give up, but he was unable to revive the Commission despite constant and strenuous efforts over the next 15 years. Sarasin died in 1929, with no sign that his vision of an international conservation organization would ever become a reality. Inspired by Sarasin's work, similar initiatives were launched in the 1930s, but these also withered and expired without effect. The onset of WWII effectively brought an end to further discussion or development of Sarasin's vision.

FIGURE 1.10. Paul Sarasin, Swiss scientist and international statesman of conservation, who founded the Swiss League for Nature Protection and whose vision of an international conservation network eventually led to the formation of the International Union for the Conservation of Nature (IUCN). (Photo courtesy of Image Archive ETH-Bibliothek Zurich.)

In October of 1944, with the end of WWII in sight, US President Franklin Delano Roosevelt proposed a meeting of "the united and associated nations [for] the first step towards conservation and use of natural resources." In a memo to his Secretary of State, Cordell Hull, Roosevelt wrote "I am more and more convinced that conservation is a basis of permanent peace" (quoted in Holdgate 1999:15). Roosevelt did not live to see his ideas bear fruit, but his vision and initiatives contributed to the formation of the United Nations (UN) in 1948. The formation of the UN brought with it the formation of two UN programs, the United Nations Educational, Scientific, and Cultural Organization (UNESCO) and the United Nations Environmental Programme (UNEP), both with strong interests in conservation. UNESCO and UNEP began to provide the international forums and multinational networks that brought conservation to the international agenda.

With the establishment of an international forum for global conservation issues, UNESCO's first director, the British biologist Julian Huxley, revived Sarasin's vision of an international, non-governmental conservation organization dedicated to networking the global conservation effort. Although Sarasin's International Commission for the Protection of Nature had not survived, the Swiss

League had, and its representatives, along with leading conservationists from other countries, pressed Huxley to revive the Commission under the auspices of the UN. Working with an existing organization, the International Council of Scientific Unions (ICSU), leaders of the Swiss League and others labored with Huxley over a period of 2 years to convene an international conference at Fontainebleau, France in 1948. The conference was attended by representatives of 23 governments, 126 national institutions and eight international organizations. On October 5, 1948, most of the delegates present signed a formal act creating the International Union for the Protection of Nature (IUPN). The Union was to "encourage and facilitate cooperation between Governments and national and international organizations concerned with, and persons interested in, the 'Protection of Nature' … promote and recommend national and international action …" to preserve wildlife and "collect, analyze, interpret and disseminate information about the 'protection of nature" (Holdgate 1999:33). This was tall order for an organization with no financial endowment, permanent budget, or, at the moment, full time employees. It put forward an entirely new organizational model, the ***Governmental and Non-Governmental Organization*** (***GONGO***), whose members and contributors would not be individuals but nations and organizations. Supported, at least in spirit, by UNESCO, the IUPN initially pursued two simple but critical objectives. First, create a working worldwide network of conservationists who would use the Union as their primary mechanism of information exchange. Second, convene conferences that would regularly reinforce such exchanges. Eventually articulating its mission more clearly through carefully framed goal statements, the Union began its work. Its first major strategic success was the creation of the "Survival Service" in 1950. Working with a grant of all of US$2,500, the Survival Service began to draw in volunteer scientific experts to write reports on the conditions of endangered species around the world. Although it had no money to fund field investigations, its reports drew increasing respect, and alarm, in the international community as the Union patiently and persistently documented the plight of global endangerment. Working directly with government representatives from many nations, the Union began to have success in its direct appeals to national leaders to work to conserve endangered species within their boundaries.

Now, more than 50 years later, IUPN has changed almost everything about itself, including its name (now the International Union for the Conservation of Nature, or IUCN), its logo (Figure 1.11), and its programs (the Survival Service eventually became the Species Survival Commission). Its once disparate reports now are published comprehensively as the world famous Red Data Books, the authoritative standard as the global "Endangered Species List" of plants and animals. What the Union has not changed is its mission. Today the IUCN, now better known as the World Conservation Union, has effectively achieved the vision that Paul Sarasin pursued but never lived to see: a worldwide union and network of conservation efforts to preserve biodiversity, and perhaps the world's most influential and respected private conservation organization. In addition to its direct efforts, its networking and information services have made thousands of other conservation organizations more effective, and stimulated the creation and development of thousands of new organizational efforts. In many ways and by a variety of measures, IUCN has been the single most important factor in the development of a truly worldwide conservation effort.

Figure 1.11. The evolution of the official logo of the International Union for the Conservation of Nature (IUCN), from the original "Flaming Artichoke" or "Brussels Sprout," as nicknamed by early IUCN staff, adopted in 1954, the "Letter Block" design adopted in 1997, and the current official emblem, adopted in 1992. (Courtesy of IUCN.)

For all its achievements, current members of the IUCN would be the first to admit that organizational success is not the same as conservation success. The threats to biodiversity that IUCN was established to combat have grown more serious. The future of conservation will not be determined only by scientific expertise, but by engagement of ordinary citizens with models of conservation appropriate to and workable in their own nations and cultures. To achieve this, the world conservation effort must adapt its traditional and, in some circles, revered historical models of nature preservation to changing conditions and circumstances. We turn back to those models of scientific conservation and sustained yield, the "Yellowstone Model" of the national park, and the "Wilderness Ideal" to see how their adaptation, and, in some cases, replacement in other cultures drives the development of conservation today.

1.5. Conservation in the Developing World: New Expressions of Resource Management, National Parks and Nature Preserves

In India, sacred forests had been protected from hunting, logging, and other forms of destructive use for over 2,000 years based on the Hindu belief that each forest was the dwelling place of a diety (Apffel-Marglin and Parajuli 2000), and such protection was effective even though the forests were often surrounded by areas of dense human habitation (Holdgate 1999:2). British colonization of the Indian subcontinent in the eighteenth and nineteenth centuries brought with it very different rationales for and approaches to forest conservation. Under the successive administrations of German forest scientists, Dietrich Brandis, Wilhelm Schlich, and Bertold von Ribbentrop, government foresters in India confidently followed the path of conservation through intensive, sustained yield management, converting thousands of acres of diverse, species-rich native Indian forests to single-species plantations of economically desirable trees. Although such an approach maximized timber production, the associated revenues and other benefits went primarily to industry and government, not local citizens. The German model, outstanding as a timber production paradigm, destroyed the resource base for local extractive economies and subsistence agriculture which had developed over many centuries. Unfortunately for local citizens, Indian independence from Great Britain did not immediately change forestry practices. By the 1990s, one study determined that 130 years of state (whether Indian or British) forest management had left the forests in worse shape than when "scientific forestry" first appeared. The investigators noted ruefully that, by this time, 22% of the nation's land was still controlled by the Forest Department, but less than half of that had any trees on it (Guha 2000:41). As one Indian noted, remarking on the effect of scientific forestry on the actual conservation of native biodiversity and cultural practices,

> *Small landowners who could not subsist on cultivation alone used to eat wild fruits and [berries] and sell the leaves and flowers of the flame of the forest and the mahua tree. They could also depend on the village ground to maintain one or two cows, and two to four goats, thereby living happily in their own ancestral villages. However, the cunning European employees of our motherly government have used their foreign brains to erect a great superstructure called the forest department. With all the hills and undulating areas and also the fallow lands and grazing grounds brought under the control of the forest department, the livestock of the poor farmers do not even have place to breathe anywhere on the surface of the earth.*
>
> (quoted in Guha 2000:39)

It was not merely scientific conservation that stood accused. As noted earlier, the Yellowstone Model of the national park was easily exportable to nations that possessed large land areas relatively unaffected by human development, especially where such land was either uninhabited or where the inhabitants had no standing as citizens and therefore could be forcefully relocated. Not surprisingly, the first countries to imitate the US model were Australia, South Africa, Canada, and the Scandinavian countries of Europe. The concepts of national parks and wilderness areas, which these countries adopted, viewed the human presence as destructive, something to be excluded if the "real" values of nature were to be preserved. This destructive view of human impact, however, was not one that could be exported to the densely peopled and much altered landscapes of western Europe or southeast Asia. The US model was inapplicable in settings like western Europe, where humans had been resident on land and affected it for centuries, such that there were no large undeveloped tracts left, or in Central America, where there was little undegraded land remaining. In countries where primitive indigenous peoples had lived on the land without "developing" it for millennia, the "Yellowstone Model" was not only inappropriate but unjust, forcibly removing thousands of individuals from their homes, native landscapes, and cultural practices in the name of conservation. As environmental scholar Ramachandra Guha noted regarding the establishment of game reserves and national parks in the Republic of South Africa, "Where did the African fit into all this? To be precise, nowhere.… In game reserves Africans were barred from hunting, while in national parks they were excluded altogether, forcibly disposed of their land if it fell within the boundaries of the designated sanctuary" (Guha 2000:46–47).

The final pillar of North American conservation, the "Wilderness Ideal," also proved problematic in other cultural settings. In the United States, designated wilderness areas were established on much the same grounds as national parks, except without developments for the comforts of visitors. US conservationists have tended to conflate wilderness and park preservation, and the absence of permanent human presence, with biodiversity preservation. As conservation biologist Sahotra Sarkar has noted, two problems are created in developing countries when the Yellowstone Model and the wilderness ideal are employed uncritically. First, local populations are displaced and their economies disrupted or destroyed. Second, conservationists fail to see that high levels of biodiversity may be in areas with high densities and long land tenures of indigenous peoples, whose historic practices of farming and resource extraction may actually be beneficial to biodiversity enhancement (Sarkar 1999). As such, conservation strategies must be rethought in cultural context, and their objectives clarified, because wilderness preservation and biodiversity conservation approach similar issues with very different goals, strategies, justifications and targets (Table 1.1) (Sarkar 1999).

As conservation has increasingly become an international effort, new models of nature preservation, facilitated by international programs like UNESCO, UNEP, IUCN, and others, have replaced traditional approaches. The Man and Biosphere Program, begun in 1970 under the auspices of UNESCO, has provided a mechanism for establishing the equivalent of "world national parks", but in a manner very different from the Yellowstone Model. The Man and

Table 1.1. Contrasts between key conservation issues in wilderness preservation and biodiversity conservation.

Issue	Wilderness preservation	Biodiversity conservation
Objective	Landscapes without humans	Biological diversity at all levels of organization
Justification	Aesthetic	Intellectual interest; present and future utility
Targets	National parks; wilderness preserves	High-biodiversity regions; representative sample of biodiversity
Obstacles	Economic interests; overconsumption; human encroachment; invasive technologies	Economic interests; overconsumption; human encroachment; invasive technologies; habitat fragmentation; human exclusion
Strategies	Legislation; habitat purchase	Diverse methods

Source: Developed from concepts from Sarkar 1999. Table design by F. Van Dyke.

Biosphere Reserves establish various "zones" within the protected area. An inner protected "core" in the preserve permits little or no disturbance. Bordering this, buffer zones or traditional areas permit local residents to conduct carefully controlled commercial and subsistence activities. Beyond this area, outer buffer zones are managed to permit increasing use and development of natural resources, often following a paradigm of "scientific conservation," but this time fully informed by the knowledge of local cultural practices and expertise. Many Biosphere Reserves also have research areas, where new types of land use and habitat management can be carried out on an experimental basis, fulfilling the visions of Doane and Leopold that "wilderness" areas, or, in this case, even not-so-wilderness areas, may prove important laboratories to aid scientific understanding. Again, unlike US and European models, Biosphere Reserves often permit and engage a great deal of local participation in the management of the preserve, not simply relying on centralized government control or scientific expertise.

1.6. Return to Start: What is the Place of Conservation Biology in the World Conservation Effort?

1.6.1. The Emergence of Conservation Biology from the Applied Sciences

If conservation is only a moral or political cause, then some would argue it hardly needs a separate science to support it. The classical disciplines of biology, chemistry and physics, supported by the more recent but now well established applied sciences like forestry, wildlife management, and fisheries management, would be sufficient to inform policy makers and activists to make the right decisions and support the right causes. Indeed, some of the world's most influential conservationists have strengthened, and in some cases even founded, such classic or applied disciplines. What is the function of conservation biology as a professional scientific discipline, and does it possess sufficient distinctions to endure as a discipline in the years to come, rather than being absorbed into existing lines of study?

Through the work of Leopold and others, applied sciences in resource management gained academic respectability in state universities after the 1930s. The most pervasive and influential of these disciplines included forestry and silviculture, fisheries management, (outdoor) recreation management, range management, and wildlife ecology (the modern version of game management). In addition, the traditionally "pure" discipline of ecology increasingly featured studies of species or systems with clear implications for conservation. The inaugural issue of the *Journal of Wildlife Management* (JWM), the official journal of The Wildlife Society (TWS), defined wildlife management as "the practical ecology of all vertebrates and their plant and animal associates" (Bennett et al. 1937). In fact, the lead article of the inaugural issue actually conflated wildlife management and conservation biology as one and the same, saying "In the new and growing field of conservation biology …" (Errington and Hamerstrom 1937:3). Early issues of JWM in the 1940s showed promise of embracing this definition, featuring a number of multiple-species studies and non-game studies (Bunnell and Dupuis 1995). However, in the decades that followed, JWM and TWS became increasingly dominated by studies of game mammals and birds.

The applied sciences of wildlife management, forestry, fisheries management, range management and others were hindered from embracing studies of biodiversity and multiple species in other ways besides their emphasis on economically valuable species and commodity uses of resources. Their paradigm of conservation science, developing initially in the United States, rested primarily on two intellectual pillars. One was studies of individual species of interest to conservation. The other was the study of individual types of habitats. Under this approach, conservation was essentially a case by case effort. Effective conservation was based on knowing everything possible about the natural history of the species of interest and then preserving as much of its habitat as possible. Refuge design for wildlife was typically based on preservation of habitat for a particular species, whether it was the Kirtland's warbler (*Dendroica kirtlandii*) on specially purchased land in Michigan, the snow goose (*Chen caerulescens*) at DeSoto National Wildlife Refuge in Iowa, or the Joshua tree (*Yucca brevifolia*) at

Joshua Tree National Monument in California (Figure 1.12). Understanding the natural history of a species and its patterns of habitat use were considered the first steps in any conservation plan (Simberloff 1988). Such effort was intelligent and sincere, but did little to establish general principles that could be applied to all species or to produce unifying theories of refuge design.

Despite these problems, and despite their tendency to emphasize game species over nongame species, the applied sciences in general and wildlife ecology in particular prospered in the climate of a growing environmental and conservation movement of the 1960s and 1970s. Legally supported by laws like the US Endangered Species Act and aided by associated funding, studies in wildlife ecology and management became increasingly important as sources of scientific information for management and recovery plans for threatened animal populations. Wildlife ecology, although continuing to emphasize studies of animals that were hunted or trapped for profit or recreation, expanded to include specialties such as “nongame wildlife management” and “urban wildlife management.” Wildlife ecologists and managers also increased their focus on conservation issues, to the point that traditional wildlife biologists wrote textbooks on “biological conservation” and started a journal with the same name.

Although the applied sciences were becoming more inclusive in their definition and conception of “wildlife,” tensions between the applied sciences and the conservation movement were growing. With prophetic insight, Aldo Leopold had foreseen these tensions decades earlier and predicted the outcome. In an essay titled, “Land Health and the A-B Cleavage” (Leopold 1966), Leopold wrote that there was a single (A-B) cleavage common to many of the academic specialties in resource management. “Group A,” wrote Leopold, “regards the land as soil, and its function as commodity production; another group (B) regards

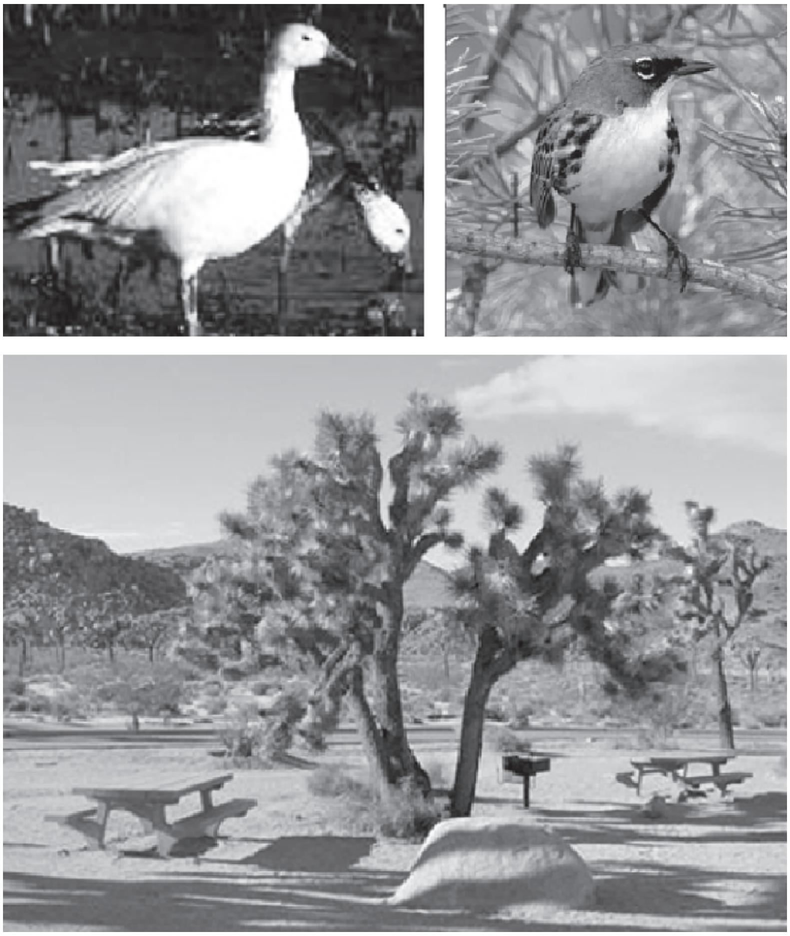

FIGURE 1.12. Three species, snow goose (*Chen caerulescens*, top left), Kirtland’s warbler (*Dendroica kirtlandii*, top right) and Joshua tree (*Yucca brevifolia*, bottom), which have been the focus of special management areas, refuges, or national monuments in the US designed primarily for their benefit. (Snow goose photo courtesy of US Fish and Wildlife Service. Kirtland’s warbler photo courtesy of US Forest Service. Photo by Ron Austing. Joshua tree photo courtesy of US Geological Survey.)

the land as biota, and its function as something broader" (Leopold 1966:258–259). Resource management fields such as wildlife management, forestry, and range management (the A group) did not fully embrace either the values espoused by Leopold and others or the growing emphasis on nongame species. Although many biologists in wildlife management and other sciences respected Leopold's ethical position that valued all species in the context of their communities, the bulk of money and effort consistently went toward enhancing populations of species with commercial or recreational value for humans (Soulé 1985).

The A-B cleavage was not confined to a single field, such as wildlife management, but was pervasive throughout the applied sciences. The 1960s and 1970s had seen the development of major new ideas in population biology and community ecology, such as the theory of island biogeography. Many scientists began testing the predictions of the new paradigms in the problems of conservation. But the results of their experiments were not always appreciated in traditional applied sciences such as wildlife ecology, fisheries management, forestry, and range management. These disciplines had become departmentalized in major universities and isolated from one another. Their isolation led to alienation and even hostility. The natural exchange of ideas and infusion to applications in conservation problems was inhibited (Soulé 1986).

The traditional academic disciplines in resource management were also limited in other ways. For the most part, they did not understand or effectively respond to the growing chorus of voices in the developing field of environmental ethics that claimed that all species, not merely game animals and fish, livestock, or plants of commodity value, possessed intrinsic values, not merely utilitarian values. Conversely, active conservationists (Leopold's "B" group) were failing to infuse their land ethic into resource management and the academe. Stress on Leopold's A-B cleavage was increasing, and the pressure could only be relieved by a split. But even as this tension was preparing academia and the conservation movement for the emergence of conservation biology, the foundational discipline of both – namely ecology – was undergoing significant paradigm shifts that would help to create the need for a new discipline with a radically new perspective. With these shifts in scientific emphasis and approach emerged an array of conceptually distinctive traits unique to the new discipline.

1.6.2. Conceptually Distinctive Characteristics of Conservation Biology

Conservation biology has been described as the science of scarcity and abundance, and more precisely defined as "application of biology to the care and protection of plants and animals to prevent their loss or waste" (Meffe and Carroll 1997). This statement is a reflection of one of the most distinctive characteristics of conservation biology. Born out of the crisis of worldwide extinctions and loss of species, the first and most important distinction of conservation biology is its focus on the preservation of biodiversity (the entire range of all species, their habitats, and their phylogenetic lineages), not on the management of individual species. Core disciplines that inform conservation biology's attempts to achieve this goal are, according to Soulé (1985), ecology, systematics, genetics, and behavior. Related disciplines in the applied sciences, such as wildlife ecology, fisheries management, forestry, and range management also draw much of their source data from similar backgrounds. However, the latter fields have traditionally selected subjects for research on the basis of either common characteristics or common applications for their management. Conservation biology, in contrast, focuses on the study and preservation of the diversity of life itself.

Conservation biology's second distinction as a scientific discipline in that it is both *value laden* and *value driven*. Integral and distinctive to conservation biology's identity as a discipline is its explicit recognition of Michael Soulé's four "normative postulates" (Soulé 1985). The first is that d*iversity of organisms is good*, and its negative corollary is that *the untimely extinction of populations and species is bad*. Second, *ecological complexity is good*. The second postulate assumes the first postulate, but explicitly adds value to the preservation of habitat and ecosystem diversity. Thirdly, *evolution is good*, or more precisely, that it is desirable to maintain the genetic potential of populations that permits adaptation and innovation in a changing environment. Soulé's final postulate is that *biotic diversity has intrinsic value, regardless of its utilitarian value*. Stating this as a normative value makes it explicit that conservation biology is committed to the study and understanding of all species and their relationships. Although conservation biology can be described by its *interest* in biodiversity, it is defined by its *commitment* to the *value* of biodiversity. The emergence of conservation biology has been interpreted as the mandate for conservation in the scientific community, as well as a mandate for science to attempt the noble (but perilous) quest of assimilating moral principles into scientific study and application. A foundational principle of conservation biology is that species possess intrinsic value, not merely as commodities or even as objects of study, but as entities which *ought* to exist and persist in the world.

A third distinction of conservation biology, strongly related to the second, is that it is *mission- and advocacy-oriented*. In fact, conservation biology has been explicitly defined as *a mission-oriented discipline comprising both pure and applied science* (Soulé and Wilcox 1980:1). This sense of mission in conservation biology is a natural consequence of being a value-driven discipline. Given the intrinsic value of species, conservation biology perceives that the best and highest application of scientific knowledge about species is to ensure their preservation. But conservation biology does not confine this effort to research and management. Rather, many conservation biologists assert the importance of scientists being able to communicate the spontaneous inner experience and appreciation for the creatures they investigate (Naess 1986), claiming that no one has more expertise, or right, to express a love for nature than those who have given their lives to its study (Soulé 1986). Indeed, environmental philosopher Arne Naess, in his keynote address at the Second International Conference on Conservation Biology in 1985, told his audience of conservation biologists that they had "obligations to *announce* what has intrinsic value" (Naess 1986, emphasis his). As a discipline, conservation biology's emphasis on action to save species and habitats and its declared intention to announce the values of nature encourages, indeed often demands, that its practitioners act as ***focused advocates*** (Rohlf 1995) which can be defined as a person or group reporting data concerning an area in which he or she has expertise as well as deeply held convictions, and who works to ensure that the information presented is correctly interpreted and rightly applied.

A fourth distinction is that conservation biology is a *crisis-oriented* discipline. Its mission, the preservation of biodiversity, is perceived by practitioners as not merely important, but urgent, emphasizing the need for *immediate application* of scientific information for the benefit of threatened species, and the discipline's attention and choice of subjects for study is often driven by how immediately the subject is threatened with destruction or extinction. Conservation biology's need for rapid investigation and response do not always provide it with the luxury of long reflection and multiple replications of studies before action is taken. Historically, most scientific disciplines, including biology, have tended to view unfavorable or premature application of scientific results as worse than no action, and have emphasized the importance of minimizing risk and maximizing reliability. In conservation biology, however, failure to act when a population is declining or a habitat is being degraded may ensure the extinction of the species or the loss of its environment. Conservation biologists are more willing to tolerate the risk of inappropriate action than to tolerate the irreparable losses or environmental damage that may be associated with no action.

Although possessing an academic bias, conservation biology is different from many related academic disciplines in its tendency to cross disciplinary lines. This is conservation biology's fifth distinction, its *integrative and multi-disciplinary nature*. Although rooted in the core discipline of biology, studies in conservation biology routinely cross disciplinary boundaries among major taxa, such as plants and animals, vertebrates and invertebrates, and between biological and physical processes. Further, because it is value driven and mission oriented, routinely investigates and addresses issues of ethics, human behavior and culture, law, politics, and sociology.

POINTS OF ENGAGEMENT – QUESTION 2

Since the Enlightenment, Western science has presented and described itself as value neutral. Is being value neutral an expression of objectivity or apathy in conservation? Does an idea become less true if one feels personally connected to and involved in the idea's implications? Do you believe that conservation biology will continue to treat its "normative postulates" as important elements in its work, or adopt a more "value-free" approach characteristic of many other sciences? Why?

A sixth distinction is that conservation biology is *a science that is concerned with evolutionary time*. That is, in its emphasis on the preservation of biodiversity, conservation biologists seek not merely the preservation of present *types* of organisms, but the preservation of their genetic heritage (representing their evolutionary history) and the preservation of ecosystem processes that promote adaptation, innovation, and speciation to maintain and enhance future biodiversity.

A seventh distinction of conservation biology is that it is an *adaptive* science, unapologetically imperfect and, at times, imprecise. Although the recent paradigm of *adaptive management* is not unique to conservation biology, it is a concept uniquely at home in this discipline. Compared to more traditional, management-oriented disciplines in the life sciences that have tended to see management actions and their responses in a cause-and-effect relationship, conservation biology is characterized by its tendency to treat management actions themselves as experiments. It tends to both expect and accept a higher degree of uncertainty associated with the response of a system or a population. The response is then treated more as an experimental result than a perfectly predicable outcome, and the management strategy itself is adaptively revised in light of the results obtained.

1.7. Synthesis

Conservation biology is inexorably wedded to conservation, a movement that is informed by science, yet seeks normative ends and purposes as "good." The initial attraction of scientists to conservation biology's most explicit professional expression of itself, The Society for Conservation Biology, was indicative of the growing dissatisfaction scientists felt with being mere "informers" about the state of the biodiversity crisis instead of actors who could do something about it. To be able to persist as a distinct discipline, conservation biology needed more than a crisis in biodiversity and a few new scientific ideas. To survive and grow, a discipline requires a unique conceptual framework and a set of identifiable intellectual distinctions. "Disciplines," noted Michael Soulé, "are not logical constructs; they are social crystallizations which occur when a group of people agree that association and discourse serve their interests. Conservation biology began when a critical mass of people agreed that they were conservation biologists" (Soulé 1986:3).

The roots of conservation historically have been grounded in moral arguments about the intrinsic value of nature, the proper response of humans to nature, and the rights and needs of future generations to enjoy nature and the resources it provides. Although the conservation movement dare not be ignorant of the best scientific information and insight, conservation biology dare not be ignorant of its own origins, and the motivations of individuals like Gilbert White, John Muir, Theodore Roosevelt, Aldo Leopold, Paul Sarasin, Michael Soulé, and others who, although well informed of scientific theories that could make conservation effective, also understood logical and moral arguments that made conservation worth doing.

Conservation biology is a product of such past and continuing efforts in conservation, and must be presented and understood as a unity of facts, theories, and values linked together by common purpose. Indeed, the environmental economist Herman Daly rightly called conservation "a policy in the service of a purpose" (Daly 1999:694) and I will not dispute his insight. The chapters that follow will identify the controlling ideas, scientific theories, and definitive studies that today characterize and define conservation biology and its efforts to preserve biodiversity at genetic, population, and system levels. The task preliminary to these, which we take up in Chapter 2, is to carefully analyze and understand the bases of values and ethics in conservation that play a significant part today, as in the past, at directing the efforts and applications of conservation biology in a world where the threat of biodiversity loss remains ever present and growing. The question we next address is: why should we value the biodiversity that conservation biology attempts to preserve?

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2

Values and Ethics in Conservation

> *Future historians will find our century remarkable for its breadth of knowledge and narrowness of value judgments. Never have humans known so much about, and valued so little in, the great chain of being.*
>
> Holmes Rolston III 1986:114

In this chapter, you will learn about:

1. **Characteristics that distinguish major categories of value in conservation**
2. **Methods for determining economic values in conservation**
3. **Philosophical, cultural, and religious traditions that affirm instrumental and intrinsic values of species, biodiversity, and natural objects, and their engagement in the global conservation effort**

2.1. What Does Science Have to Do with Value?

2.1.1. Avoiding the Absurd – Being Self-Aware of Values in Conservation Decisions

In their book, *Among the Elephants*, Iain and Oria Douglas-Hamilton describe their study of the relationship of African elephants to acacia trees in Tanzania's Manyara National Park (Douglas-Hamilton and Douglas-Hamilton 1975). The elephants were destroying the acacias in the park, and the Douglas-Hamilton's job was to decide what course of action should be taken: reduce the size of the population by having some of the elephants killed or let the animals continue to destroy the acacias. Regarding the feelings of fellow scientists working in the Park, they wrote,

> *The very desire to preserve the animals was a subjective statement of faith in the animal's intrinsic worth. It was a feeling possessed by most of the scientists there …, but they would not admit this sentiment into their arguments because it could not be backed up by facts; the right and wrong of aesthetics being imponderables not open to scientific analysis.*
>
> (Douglas-Hamilton and Douglas-Hamilton 1975:75–76)

This kind of reasoning, not uncommon among conservation biologists, leads to serious internal conflict, as well as intellectual confusion and contradiction. One is expected to believe that elephants, sea turtles, African violets, or butterflies are intrinsically valuable and therefore worth preserving, and at the same time pretend that such values are not important in determining a conservation solution that will ensure the species' preservation. Such thinking is self-deception, a kind of "doublethink" George Orwell described in his novel, *1984*, as "the power of holding two contradictory beliefs in one's mind simultaneously, and accepting both of them" (Orwell 1962:176).

One cannot learn truths about conservation biology, or gain the knowledge required to be a competent conservation biologist, by practicing these kinds of intellectual errors. As noted in Chapter 1, modern conservation efforts arose from moral arguments regarding the value of nature and the proper human relationship to it. Those who made such arguments were not deceiving themselves or others. Convinced that conservation was the right course, their intellectually consistent understanding of the value of nature and biodiversity inspired their actions, fueled their energy, and allowed them to persuade others to join their work. Those who would study and would someday practice conservation biology must understand the sources of such values, the arguments that support them, and the tools for analyzing such arguments and assessing their power.

2.1.2. Recognizing Management Actions as Value Judgments

Reflecting on the failures of deer management in US national parks to control population irruptions and promote processes contributing to ecological integrity, biologists William Porter and Brian Underwood noted that, "Whether we define ecological integrity in terms of species or processes, we must inevitably make a decision as to where in the irruptive sequence we choose to intervene. That choice represents a value judgment. Although the connotation often associated with value judgments is negative, such decisions are the essence of management and cannot be avoided" (Porter and Underwood 1999:6).

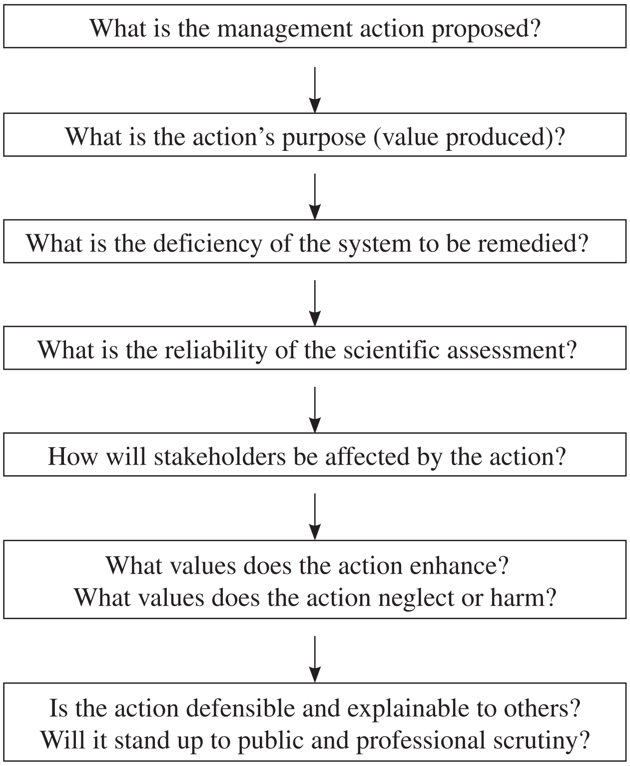
To explore the claim that management actions reflect value judgments, let us begin by defining "management" in a conservation context as *human action taken to remedy a deficiency in a system as informed by scientific assessment*. Consider a very typical case of "ordinary" conservation management on public lands. A range manager, informed by best available scientific data, decides to burn a section of sagebrush in an area used by elk as winter range (Figure 2.1). Her intention is to enhance forage production and quality for this species during a particularly stressful period of the year. Ongoing studies reveal that forage production on the winter range is low, and so is the population growth of the elk using it. The action thus meets all criteria of our above definition. The site of the burn is located in a management unit that policy-making supervisors have designated as "elk habitat," (i.e. an area in which management is to give priority to the needs and welfare of elk) and, thus, the action is a specific and particular enforcement of the "rule" established by the policy: increase the production of resources that benefit elk.

As benign and ordinary as this management action may appear, it is fraught with ethical implications. First, what is the purpose of the management action? That is, what value will be produced as a consequence of completing the action, in this case, burning sagebrush? Second, what is the deficiency of the system that we are

FIGURE 2.1. A prescribed fire in sagebrush habitat in south-central Montana, USA. Even a seemingly ordinary or "neutral" management decision represents a manager's value judgment about how and when to intervene in an ecological system, and therefore is fraught with ethical choices and considerations. (Photo by the author.)

trying to remedy? Here the deficiency is low forage production for elk. Is that deficiency important, and how reliable is our scientific assessment of it? Third, which stakeholders have legitimate interests in the state of this system, and how will they be affected by this management action? Every manager has legitimate duties, obligations, and trusts to fulfill to various stakeholders who have a vested concern in the state of the system being managed. Sometimes these duties are implicit and assumed, as with a manager in a government agency with social and civic obligations to the public. Sometimes they are explicit and even contractual, as in the case of a manager who works for the members of a private conservation organization, or an environmental consultant who is paid by a client to offer an informed recommendation. But whether implicit or explicit, there are always obligations to be fulfilled by the manager to stakeholders in every management action. Fourth, what kinds of values does the management action endorse or enhance, and what kinds of values does it neglect or diminish? In this example, the prescribed fire is likely to generate more forage for elk, but it will reduce habitat for species that are sagebrush specialists, like the Brewer's sparrow (*Spizella breweri*) or the sage grouse (*Centrocercus urophasianus*). Finally, when the action has been completed and the manager gives an account of what she did, will she be able to defend her action and explain, to any audience, why she choose one action over another?

We can visualize the process sequentially, the better to see its ethical implications.



Such questions are appropriate to every management action in conservation biology. There are no exceptions. Because this is true, every conservation biologist needs to understand how to categorize and evaluate different categories of values, as well as the ethical systems in which they are embedded. That is the subject we now take up.

2.1.3. Values and Ethics – Definitions and Initial Assessments

Value refers to a general *basis for an estimation of worth*. Values represent judgments of relative worth, merit, usefulness, importance, or degree of excellence. Values can justify and explain concrete objectives, such as conserving biodiversity, but they are not the same as the objective. ***Ethics*** are *systematic organizations of values* that establish principles for conduct and behavior. Choices we make today about what is valued will determine the range of experiences in the natural world available to future generations. Therefore, conservation biologists need a thorough and sophisticated understanding of values and ethics – two indispensable elements in conservation.

Many years ago Robert Disch produced an anthology of essays called "The Ecological Conscience" (Disch 1970). People thought the title strange then, and many still think so now. As environmental ethicist Holmes Rolston III put it, "…the moral noun does not regularly take a scientific adjective" (Rolston 1986:12). Likewise, a discussion of values and ethics in conservation biology may seem out of place, an act of trying to put scientific adjectives in front of moral nouns. For one thing, no set of scientific facts, even scientific facts about endangered species or degraded ecosystems, by themselves, entails any statement of moral evaluation or moral prescription. That is, one cannot argue from a descriptive premise (about what something *is*) to an imperative conclusion (what *ought to be done* about a particular condition) because one cannot argue logically that because something *is* (that is, something exists) that the same something *is good* (it *ought* to exist). It is common for people, including conservation biologists, to make this mistake. This error is so common that it has its own name, the ***naturalistic fallacy***, the error of arguing for what ought to be based on the facts of how things are.

A further tension between science and ethics is that, since the Enlightenment, science has been viewed by scientists and non-scientists alike as "value free." In this view of science, facts and truth are not affected by the convictions, commitments, or biases of the investigators. In the words of ethicist C. S. Lewis, such "value-neutral" science separated "the world of facts without one trace of value, and the world of feelings without one trace of falsehood, justice, or injustice … and no *rapprochement* is possible" (Lewis 1947:30–31). Just as facts were seen as value free, values were non-factual, unverifiable, and subjective.

Value-neutral science also implied that scientists should not advocate particular applications of science to specific problems because the role of the scientist was to supply value-neutral information and expertise. Advocacy represented a commitment to particular (and non-factual) values, a loss of objectivity, and a loss of reliability of scientific information. The application of science to particular problems and the advocacy of particular solutions were left to ethicists, political officials, and religious leaders.

This view of science was fundamentally flawed from its inception and has become increasingly unworkable in producing effective interaction between science and the modern world. The most serious problem of this view was in making objectivity (the accurate perception of reality) synonymous with neutrality (not engaged to, committed, or discerning of value, truth, or worth). Conservation biology emerged as a distinct discipline when a body of scientists deliberately renounced the division between facts and values and rejected the conflation of scientific objectivity with neutrality. Although committed to objective truth, conservation biologists insisted that truth informs decisions of value, and leads to specific commitments of value in the application of science to conservation. In such a context, conservation biology asserted its identify as a "value-laden, mission-driven science" and committed to the "normative postulates" of conservation biology (Chapter 1): (1) *diversity of organisms is good*, (2) *ecological complexity is good*, (3) *evolution is good*, and (4) *biotic diversity has intrinsic value*, *regardless of its utilitarian value* (Soulé 1985). To be useful, such normative postulates must be informed by specific and practical knowledge of individual conservation dilemmas. Any normative postulate, isolated from other considerations and pursued exclusively without regard for them, would bear results that would be emphatically "not good." For example, acts of introducing non-indigenous species into a system to achieve a short-term increase in the system's diversity might eliminate native species and alter ecosystem structure and function. Although such normative postulates are valuable guides for identifying the fundamental values of conservation biology, they are not substitutes for intelligent management informed by knowledge about particular systems.

Normative postulates are non-empirical statements. They are not statements of metaphysical objectivity, verifiable by experimental analysis. This fact leads some to claim that they cannot be "proven" to be "true" and are really only statements about the personal feelings of those who make them. Such a view of truth, which defines knowledge as consisting solely of descriptions of physical entities, is severely constricted, and one in which conservation biology would not be able to engage in conservation. In practice, conservation biologists seek application of the knowledge they gain from empirical studies, which demands choices. Every choice requires a decision about what is "good" or "best" to achieve a given conservation goal. Conservation derives its purpose by understanding its outcomes as expressions of value. To satisfy the inherent drive for application intrinsic to conservation biology and to express management applications in terms of norms, conservationist biologists must possess a coherent system of values that they can universally and persuasively articulate to anyone. Further, conservation biologists must be able to express such values as something more than their own personal preferences, likes and dislikes about their favorite species or their preferred state of nature. If they fail to recognize the necessity of coherent expressions of value, and fail to affirm that statements of value are statements about truth, about how things really *ought* to be, they will be left with no arguments to offer except those that express conservation as ratios of human benefits and costs. Some conservationists believe that all values should be expressed this way, but many would argue that some conservation values exist independent of human welfare and that such values should be pursued regardless of their cost. Indeed, many conservation laws such as the US Endangered Species Act explicitly state that economic considerations may *not* be used to decide whether to adopt a particular action or policy, such as listing a species as endangered or threatened. Coherent value systems that can guide applications of conservation are diverse, but persistent effort to understand such systems reveals the need to explain applications and goals of conservation as more than personal preferences.

POINTS OF ENGAGEMENT – QUESTION 1

Another scientist wrote to me saying, "People choose to study snakes because they love snakes." He went on to argue that such affection generated its own "mission," and such mission generated its own advocacy for snake conservation. Is personal affection a sufficient basis for conservation mission and advocacy or an adequate frame of reference for discourse with other scientists and the public?

2.2. The Problem of Categories: How Do We Classify Different Kinds of Conservation Values?

2.2.1. An Overview of Value Categories

There is no single universally accepted method of categorizing conservation values, but we will begin with a simple dichotomy between ***instrumental*** and ***intrinsic values***. Instrumental values measure the usefulness of a creature or object in meeting a need or providing a service to another, usually a human, and thus facilitating human welfare or happiness. Intrinsic values reside within an object itself. In other words, something has intrinsic value if it is "valuable *in* and *for* itself – if its value is not derived from its utility, but is independent of any use or function it may have in relation to something or someone else (Callicott 1986:140, emphasis his). Within these larger categories, specific sub-categories exist for natural objects in general, and for species in particular (Figure 2.2). Intrinsic value in nature, or "natural intrinsic value," is present in "some natural occasions without contributory human reference" (Rolston 1986:110). Conservation biology acknowledges instrumental and intrinsic values of species, and each merits further analysis.

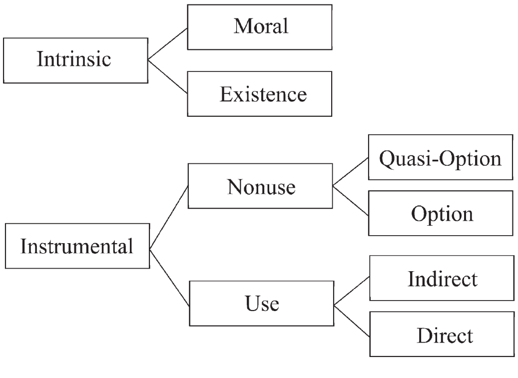


FIGURE 2.2. Categories of value and their relations. (Diagram by M. J. Bigelow.)

2.2.2. Instrumental Values

2.2.2.1. General Considerations

All human cultures are sustained through natural capital, including goods and services derived from living organisms, so instrumental values play a prominent role in any discussion of the value of non-human creatures. The most common method of estimating the instrumental value of goods is through economic analysis. Economics is the study of how people allocate scarce resources – including biotic resources – among competing ends to satisfy unlimited human wants. Biotic resources supply all food for humans and, directly or indirectly, most of our fuel and medicines. Plants are the primary source of human clothing and structural materials, and are used to beautify personal property, enhance land values, and reduce soil erosion. In unmechanized cultures and societies, animals provide services through their labor in agriculture and transportation. In human entertainment and recreation, plants and animals play significant roles in increasingly varied and economically important ways.

Biotic resources, however, also are scarce resources, and their use can be increased only at the cost of foregoing something else that is valued (Randall 1986). All biotic resources are potentially renewable resources, yet also potentially degradable and exhaustible. Even though the interests of economics and conservation often appear at odds with one another in specific cases, conservation biology and economics have fundamental interests in common, especially on the issue of species preservation. As economist Alan Randall stated, "Since species survival is a precondition for the use of the species as a resource, the preservation problem in principle precedes all other biotic resource issues" (Randall 1986:79).

Economists attempt to estimate the market value of resources, including biotic resources, through evaluation of resource scarcity (supply) and the amount of satisfaction the resource provides for humans (demand). Historically, economics has been used in making decisions in conservation, even when such decisions involve judgments about what is "right" and "wrong." Originally a branch of moral philosophy, economics only later emerged as an independent discipline (Kelman 1986). Although no longer considered a realm of moral knowledge, contemporary economic evaluations often influence what society believes is "right" in decisions on conservation.

The economic valuation of biotic resources often can be done through normal market processes. In economics, ***market goods*** can be exchanged through some form of standard currency in an economic market. Some biotic resources, such as game animals, timber, or rangelands, can be treated and valued as market goods, and their market value can be assigned with relative precision. This valuation is easiest when the value of the resource is measured in utilitarian terms, usually as some type of commodity. In that case, biotic resources often can be treated as ***private goods*** (i.e., goods that can be bought, sold, and enjoyed solely by the buyer and seller). Natural resources also can serve utilitarian values as ***public goods***, goods that are accessible to all and provide benefit to all, usually with the cost shared among the beneficiaries, such as clean water. Every choice for a particular use for a specific resource comes with inherent benefits and costs. Such benefits and costs may be direct (accrue directly to those using the resource) or indirect (accrue to others affected by the way the resource is used).

A resource economist would argue that, theoretically, all instrumental values of resources could be evaluated economically. Evaluation is easiest when biotic resources are valued as private goods, but becomes more complex when they are valued as public goods, and still more complex when future as well as present values must be considered. But these considerations also are part of economic valuation. In economic terms, five categories of value help to refine the assessment. ***Use value***, the value derived from the actual use of a resource, usually is the easiest to measure and the most amenable to evaluation by market forces. For every use, there is a unique set of ***opportunity costs*** which represent costs, or losses, associated with the inability to use the resource to produce goods A, B, and C if the resource is being used to produce good D.

The other four categories describe different kinds of non-use values. ***Option value*** refers to the value of a resources expected future use (i.e., what a person would be willing to pay to guarantee that the resource would be available for future use). ***Quasi-option value*** is the value of preserving options, given an expectation of growth in knowledge that might lead to a future, but as-yet undiscovered or unrealized use of the resource. Quasi-option value can be conceived as a kind of "speculation value" for what an investor might pay to preserve a resource, such as a rare tropical plant, given the expectation of increasing growth in knowledge of medical applications of all plant species generally. ***Bequest value*** is the value of knowing that something is preserved for future generations. ***Existence value*** is the value of knowing something exists (Randall 1986). In other words, the object is not something you are going to use now or in the future, but you derive pleasure and satisfaction simply from knowing that it is there. Various tools are used to identify values and their relative importance in a given context.

2.2.2.2. Determining Attitudes with Sociological Surveys

One way that researchers attempt to assess underlying attitudes that reflect human values of wildlife and other natural resources is through surveys. Surveys may consist of "closed-ended" questions (in which the respondent selects a particular answer or a numerical value that best represents her answer) (Table 2.1) or in-depth interviews, which permit more complex responses to open-ended questions. Survey design is a professional discipline within sociology and psychology. Its details are beyond the scope of the chapter; however, some foundational principles follow: (1) the questions and potential responses of the survey must be carefully worded according to strict protocols to avoid confusion and to clarify categories of response; (2) the sample of individuals surveyed must be representative of the population and sufficiently large to avoid problems associated with random error; (3) if subgroups of the population differ in important characteristics, representation of the subgroups also must be comprehensive and sufficiently large to ensure accurate representation; and (4) if some individuals do not respond to the initial survey there must be follow-up procedures to reach them. This is the problem of "non-response bias," because non-respondents often have significantly different characteristics than initial respondents.

TABLE 2.1. Some examples of closed- and open-ended questions in a survey of human attitudes toward conservation.

Question type	Examples	Response
Closed-ended	If a conservation biologist aspires to be effective in relating scientific findings to conservation policy, it is necessary that the basis of conservation ethics be understood.	T F
	The number of animals is more important than the genetic diversity of the group.	T F
	The value of an organism should be decided by its supply and demand.	T F
Open-ended	To what extent should ethics play a role in the process of developing conservation policy?	
	How important is the genetic diversity of a population?	Variable
	What criteria should be used to assign value to an organism?	

Source: Table designed by M. J. Bigelow.

If such problems can be successfully addressed, survey data can provide insights into what people value in conservation and why. For example, Kellert investigated basic wildlife values in Japan by creating a typology of wildlife values and attitudes (Table 2.2) and then designing multiple questions and scales to measure the strengths of different attitudes in the respondents (Kellert 1991). These responses revealed that the most common attitudes of the Japanese toward wildlife were humanistic (strong affection for individual animals or particular species) or negativistic (avoidance of animals because of dislike or fear). Compared with attitudes of US citizens determined

TABLE 2.2. A typology of wildlife values and attitudes employed in assessing public attitudes toward wildlife.

Type of Value or Attitude	Definition
Naturalistic	Values that relate to enjoyment from direct contact with wildlife
Ecologistic	Values associated with the importance of a species to other flora and fauna and to the maintenance of ecosystem processes
Moral	Values associated with inherent rights or spiritual importance of species
Scientific	Actual or potential value associated with a species' contribution to enhancing human knowledge and understanding of the natural world
Aesthetic	Values associated with the species' possession of beauty or other perceived qualities admired by humans
Utilitarian	Values associated with species as sources of material benefit or use
Dominionistic	Values associated with the mastery and control of animals, typically through sport
Negativistic	Attitudes associated with the avoidance of animals because of dislike or fear
Neutralistic	Attitudes associated with the passive avoidance of wildlife because of lack of interest
Theistic	Values associated with the belief that a supernatural deity or force creates, sustains, and values wild species

Source: Kellert 1991. Table designed by M. J. Bigelow.

FIGURE 2.3. The giant panda (*Ailuropoda melanoleuca*), symbol of the World Wildlife Fund and a classic example of a "phenomenologically significant animal" (Shepard 1978) that evokes strong feelings of identification, affection, and concern in humans. (Photo courtesy of C. Kasnoff, Endangered Earth.)

in earlier studies (Kellert 1985, 1989), Japanese citizens were more dominionistic (motivated to control animals, especially in sporting activities) and less moralistic (concerned for right and wrong treatment of animals) and ecologistic (concerned for relationships of species within a system) than were US citizens (Kellert 1991).

Coupled with in-depth interviews, survey data may reveal not only attitudes of people toward wildlife and other biotic resources, but also the cultural basis and background of such views. Throughout the world, such data reveal that humans are most concerned for creatures that are large, aesthetically attractive, phylogenetically similar to humans, and regarded as possessing capacities for feeling, thought, and pain (Kellert 1986). Such species represent what have been called ***phenomenologically significant animals*** (Shepard 1978). Given such human attitudes, it is no wonder that animals in this group are often chosen as emblems for major conservation organizations such as the World Wildlife Fund (giant panda, *Ailuropoda melanoleuca*) (Figure 2.3), as representatives for government agencies like the US Forest Service (Smokey Bear), or as a country's national symbol (for the US, the bald eagle, *Haliaeetus leucocephalus*).

Survey data also can be used to assess human relationships with nature in terms of personal experience. One of the most common measures is "user satisfaction," a metric which determines the level of personal satisfaction an outdoor recreationist experiences in a particular recreational activity. The higher the satisfaction, the more the experience met or exceeded the expectations and desires of the recreationist. This measure has been used to evaluate the quality of natural environments as well as the preferences and values of those who use them (Dustin and McAvoy 1982). Such knowledge can assist conservation biologists in determining what public attitudes are toward wildlife, conservation, and natural areas. In addition, user satisfaction surveys may be valuable in designing public relations campaigns to win support for conservation goals. However, survey, interview and user satisfaction data, by themselves, do not evaluate the validity of the attitudes that they identify, nor do they help conservation biologists argue persuasively for alternative attitudes or ethical perspectives.

2.2.2.3. *Tools of Economic Valuation: Cost–Benefit Analysis and Contingency Valuation*

The most common, and sometimes legally prescribed, tool for determining the value of biotic and ecological resources in their natural state versus their value after detrimental acts of development is cost-benefit analysis (CBA). Conceptually simple to imagine, but often practically difficult to achieve, cost–benefit analysis, as its name implies, attempts to assess the benefits of a particular action and compare them to the environmental costs of that action. The preferred alternative is the one in which benefits most outweigh costs. For example, cost–benefit analyses are often associated with environmental impact statements (EIS) required under the US National Environmental Policy Act. "Costs" of the action described in the EIS typically include both short- and long-term environmental consequences associated with the proposed action. "Benefits" to species, biodiversity, or ecosystem preservation must include both instrumental values – such as game, water, range, and timber – and non-instrumental values – such as visual and scenic appeal, religious significance, or historic importance. Cost–benefit analyses also may be associated with the proposed listing of a species as threatened or endangered, with broad changes in environmental or conservation policy, or with the effects associated with new conservation legislation. Government bureaucrats, private consultants or corporations, non-governmental conservation organizations, or other individuals or groups that have a vested interest in the valuation of biotic resources might perform the actual analysis.

Cost–benefit analyses can be attractive to decision makers in conservation because such analyses attempt to translate all the values associated with a decision into a common currency, usually market value, so that diverse entities (e.g., timber values and wildlife values) can be compared directly. Such analyses also have the attraction of forcing decision makers to identify and evaluate the value of all entities affected by their decision, and place the burden of proof on those who value the preservation of biotic resources rather than on proponents of development. In CBA, defenders of biodiversity must show that species preservation is at least as economically valuable as a proposed development that is designed from the outset for market valuation and consumption.

Criticisms of cost–benefit analysis as a decision-making tool are numerous. For example, some acts that might be judged morally wrong may have high economic benefits and low costs, whereas some acts that might be judged as morally right may have low benefits and high costs, as we shall see later in this chapter in the case of orangutan conservation in Indonesia. In addition, CBA uses currencies most appropriate to private transactions of economic goods as guides for public policy, thus equating private preferences with cultural and social values. CBA assumes that preserving a species should be valued for its *human benefits* rather than as an act of *moral obligation*. The distinction is critical, and we will see why in our examination of an oft-used method for determining market values of non-market goods, like endangered species.

2.2.2.4. Contingent Valuation Analysis

2.2.2.4.1. Willingness to Pay

Determining the economic value of the satisfaction a person derives from simply knowing that a particular resource or species exists is one of the most challenging problems of economics. The ***Willingness to Pay*** (WTP) approach is one form of ***contingent valuation*** (CV) methodologies that attempt to determine the value of non-market goods by creating a "shadow market," often measured in expressed preferences, that provides an index of what the non-market good is worth. The WTP approach attempts to assign monetary worth to existence value by asking, usually through surveys, what a person would be willing to pay in exchange for the preservation of a given entity, such as a rare species, under specific circumstances. To an economist, "benefits" associated with a resource are those things that give it value, and something has value if someone is willing to pay for it, no matter what their reasons. To assess benefits of this kind, a typical WTP survey item might propose, "Suppose an undeveloped tract of tallgrass prairie at the edge of your town was found to contain a population of a rare species of butterfly. How much would you be willing to pay to keep this area from being developed and preserve the butterfly population?" The WTP approach is often made more sophisticated by giving the respondent a range of different alternatives (for example, how much would you pay to preserve an endangered bird, snake, plant, butterfly, or beetle) that allows the person to assign different valuations to different kinds or categories of species. Such contingent valuations are then used to determine preferences. The WTP approach also can be used to ask more directly how much the person would pay to keep the habitat itself in an undeveloped state, how much to have it turned into a golf course, a housing development, a water treatment plant, or a window factory. To give the question a greater sense of legitimacy and plausibility, the question may be phrased in the form of a potential bond issue, such as a state tax to preserve the habitat of an endangered species. In this form, the researcher can determine: (1) how many people would vote for the bond issue at a given level of taxation, (2) how many people would be unwilling to pay anything at all, (3) the average cost valuation of those against the bond issue but willing to pay some lesser amount (Hunter 1996), and (4) the maximum taxation rate of the bond issue likely to pass in an open election. Results are used to infer the value of a non-economic good (an endangered species) or state (an undisturbed habitat). The proposed mechanism of payment (taxes, government bonds, recreation fees, or direct cash contribution) can have a significant effect on the answer.

Some conservationists support WTP approaches because they permit normally non-economic goods, such as endangered species, to stand on equal footing with hydroelectric dams, power plants, or subdivisions. Even if

FIGURE 2.4. Hungerford's crawling water beetle (*Brychius hungerfordi*), a US endangered insect species, might generate low valuations from individuals in surveys to determine Willingness to Pay (WTP) for conservation, but its estimated aggregate value from such surveys might run into millions of dollars in the entire US population. (Photo courtesy of US Fish and Wildlife Service.)

the average US citizen would pay only 2 cents to know that the Hungerford's crawling water beetle (*Brychius hungerfordi*) (Figure 2.4) is alive and well, the valuation of this sentiment in the US population would run into millions of dollars. WTP allows economists to determine the value of non-economic goods, such as endangered species, that can lead to assessments of high monetary valuation, permitting conservationists to argue that the existence value of a species is worth more than the gains to be realized from its destruction.

2.2.2.4.2. Willingness to Accept Compensation

An alternative, related approach used in CVA is the ***willingness to accept compensation*** (WTA) method. Unlike WTP, which attempts to determine what a respondent would pay for an environmental amenity, WTA attempts to determine what the respondent would accept as compensation for losses suffered as a result of gaining or maintaining such an amenity. Like its counterpart, WTA typically uses survey methods to determine the average payment affected individuals would accept for losses they incur as a result of conservation practices. WTA can be an effective and necessary method in cases where the achievement of a conservation goal or satisfaction of an environmental amenity come with a definite and tangible cost to local residents. In fact, determining an acceptable and just level of compensation is often the only way to break otherwise irresolvable value conflicts that may arise in conservation efforts at regional or landscape scales. The reintroduction of the gray wolf (*Canis lupus*) (Figure 2.5) in Yellowstone National Park in the 1990s could not have proceeded without a compensation program established by Defenders of Wildlife, the Bailey Wildlife Foundation Wolf Compensation Trust, to reimburse ranchers outside the park for livestock losses caused by wolves (http://www.defenders.org/programs_and_policy/wildlife_conservation/solutions/wolf_compensation_trust/index.php). Likewise, fair compensation, determined by WTA, is increasingly viewed as essential in establishing national parks in developing nations where many people obtain a living from natural resources through hunting, gathering, and pastoral agriculture. For example, the establishment of Mantadia National Park in Madagascar, an area with one of the world's highest densities of endemic species, could not have succeeded without a program to compensate local residents for losses associated with changes in land use in and around the park (Shyamsundar and Kramer 1996).

FIGURE 2.5. The gray wolf (*Canis lupus*), a species that probably could not have been reintroduced into Yellowstone National Park, USA, without first determining the amount associated with Willingness to Accept compensation (WTA) among local ranchers for livestock losses to wolves, and then establishing a fund to provide such compensation. (Photo by Tracy Brooks. Courtesy of Mission/Wolf/US Fish and Wildlife Service.)

2.2.2.5. Criticisms of Contingent Valuation Analysis

Its strengths and successes notwithstanding, criticisms of the CVA approach abound from both economists and conservationists. Some economists argue that the WTP and WTA do not measure anything real because the respondent's answer is strictly hypothetical and imaginary. In WTP, for example, respondents gives up no real money or goods to express their preference and thus are likely to grossly overestimate their willingness to pay for the existence of the endangered species. This concern is supported by the fact that, in some studies, the public's combined estimated values for individual environmental entities exceeded their aggregate disposable income (Carson et al. 1998)!

The WTP approach is even more harshly criticized by environmental ethicists and conservationists. Ethicist Mark Sagoff argues that the WTP approach does not measure existence value at all, but instead confuses values with benefits. Valuations generated from WTP analysis often are used as measures of *economic benefits* of preserving endangered species. These measures are then included in cost/benefit evaluations that are used to evaluate policy decisions (whether or not to lease public land for an oil well, whether to allow housing development in a habitat used by a rare butterfly, whether to allow a wetland to be drained for farming). Most research, however, shows that respondents to WTP questionnaires are not, in their assessments of valuation, making personal estimates of the economic benefits of preserving an endangered species, rather, they are expressing the relative strength of a moral conviction that the species ought to be preserved. WTP analysis fails to make a distinction between what people value because it benefits them and what they believe is valuable for ethical reasons or on intrinsic grounds (Sagoff 2000). In other words, WTP analysis treats all values as expressions of personal preference, a mistake that is, in fact, common to all approaches that use sociological surveys. Values, as noted earlier, are *estimations of worth*, and exist regardless of the personal *benefit* they create for any individual. *Preferences* refer to our personal acts of choosing or esteeming one thing over another. That is, preferences are things people value or choose because the choice benefits them.

Fundamental confusion between values and preferences occurs constantly in sociological survey analysis, and particularly in the use of such analysis in conservation. This is an error which reduces value to "taste" and ultimately conflates value with benefit, which are two very different things. When one confuses values and benefits, it creates an ethical distortion that shifts the focus from the worth of the object (value) to an index of the respondent's self-interest (preference-expressed benefit). The WTP approach assumes that welfare is increased when preferences are satisfied. The more people are willing to pay to have their preferences satisfied, the greater the benefit, so welfare and benefits are maximized by allocating resources to those who are most willing to pay for them. As Sagoff puts it more sarcastically, "Resources should go to those willing to pay the most for them because they are willing to pay the most for them," (Sagoff 2000). Many consider this conflation of value with benefit a gross distortion of value, not an accurate measurement of it.

Such distortion can lead to a more serious problem. A conservation biologist may take up the cause of protecting an endangered species because of the perceived value in the species itself and the sense of an inherent obligation to protect it, but in public discourse, the same biologist will feel pressure to frame reasons for protecting the species in light of human self-interest. For example, the biologist might argue that future generations will be deprived of the value of knowing the species, that the species may have actual or potential market value, or that its loss will negatively affect the value of recreational opportunities, like bird watching, in its habitat. In doing this, the biologist may feel the end justifies the means, yet not realize that this approach is, in the words of ethicist Lawrence Tribe, "helping to legitimate a system of discourse which so structures human thought and feeling as to erode, over the long run, the very sense of obligation which provided the initial impetus for his own protective efforts" (Tribe 1974:1330–1331).

An example of this kind of ethical erosion can be seen in the "economic conservation" displayed in an enterprise called "sea turtle ranching." In past efforts to use market forces for the benefit of conservation, eggs of the green turtle (*Chelonia mydas*) have been taken from the wild and hatched under controlled conditions. The hatchlings were then raised to market size and used to meet the worldwide demand for sea turtle products such as leather, oil, soup, and meat. Proponents of the plan have argued that, handled in this way, "surplus" eggs find a useful purpose, some of the hatch can be released to augment remaining turtle populations, and incentive for poaching is reduced.

In his classic response to this idea, an essay entitled, "The Business of Conservation," biologist David Ehrenfeld argued that sea turtle ranching was, in fact, a pathetic combination of greed and short-sightedness (Ehrenfeld 1992). He pointed out that, apart from the myriad of problems associated with keeping and raising sea turtles in captivity, sea turtle ranching actually increases the worldwide demand for sea turtle products. Such demand not only makes greater demands on world turtle populations through legitimate egg collection, but it also makes it more attractive to poach the eggs of wild turtles. And turtle poaching will always be more profitable than turtle farming because the affluent consumers who have acquired a taste for sea turtle products cannot tell the difference between legal and illegal goods. Ehrenfeld summarizes the problem succinctly. "The power of global demand erodes all safeguards.… Thus the commercial ranching of green turtles inevitably brings us around again on the downward spiral – a little closer to the extinction of the remaining populations. By no stretch of the imagination is this conservation" (Ehrenfeld 1992:2).

Economic analysis can be useful in an assessment of the value of biotic resources, but is not equally precise in assessing all categories of value such resources might possess, so it cannot function as a comprehensive ethical system to provide meaningful value for biotic resources. Other measures and methods of value assessment and analysis are necessary to address other dimensions of species' worth, including the most fundamental question, the nature and characteristics of intrinsic value.

2.3. The Problem of Moral Value: Assigning Intrinsic Values in Conservation

2.3.1. Where Does Intrinsic Value Reside?

A fundamental question in environmental ethics is whether the ethic we are examining is an ethic *about* the environment or an ethic *of* the environment, a distinction Holmes Rolston III stressed as the difference between ***secondary environmental ethics*** and ***primary environmental ethics*** (Rolston 1986). The former see the environment as an important stage upon which the drama of human choice is played out, but the ethical decisions are really about people, and environmental entities are means to correct ethical decisions and behavior about humans. What we would call secondary environmental ethics are really simply classical forms of ethics, such as, for example, utilitarianism, being applied to environmental and ecological limitations, such as, *you should not overfish this species if you want to continue to derive food and income from it in the future*. In this view, all of nature's goods, including all her species, are really human goods. In contrast, a *primary environmental ethic* is one in which environmental entities, such as non-human species, ecosystems, or even "the land" itself is treated as a moral subject. Although such entities do not make moral choices and are not, therefore, moral agents, it is possible for human beings to treat them rightly or wrongly in an ethical sense. The existence of a primary environmental ethic would mean that non-human environmental entities possess a "good of their own" that should be acknowledged and protected, regardless of its costs or benefits to humans. In a primary environmental ethic, our example would be changed to *you ought not to overfish this species so that its kind does not perish from the Earth.*

An understanding of an environmental ethic as primary or secondary leads to another critical question. Are values human intellectual constructs that people design and manipulate or external realities that the human intellect recognizes and responds to? As noted earlier, intrinsic value resides in an object when the object is valuable "on its own," not on the basis of its utility to humans or other species. Some ethicists, not to mention many environmental economists, assert that intrinsic value is an illusion. In their view, all values are anthropocentric, residing in human consciousness, therefore, all values are human preferences and subjected to economic evaluation. All goods are human goods and all ethics are ethics about humans. A thing is good when it tends to increase utility and bad when it tends otherwise. But not all believe that this is so.

Most ethicists would admit that the *locus* of all value is human consciousness, and some would say that the perception of value in nature is an observer-dependent, secondary quality that arises solely out of the observer. But many would argue that, while the locus of all value is within the human consciousness, the *source* of all value is not (Callicott 1986). For example, philosopher Donald Regan illustrates one concept of intrinsic value with a natural object – the Grand Canyon – and a hypothetical person – Jones. The intrinsic value of the Grand Canyon, argues Regan, is formed by the Grand Canyon itself, Jones' knowledge of the Grand Canyon, and Jones' pleasure in her knowledge of the Grand Canyon. Regan contends that there is value in the object apart from human perception of it, and that human perception adds value to it. We are given incentive, reason, and moral obligation to preserve objects that we know about in order that we may learn about them and enjoy our knowledge of them (Regan 1986).

Regan's analysis can be displayed and better understood with the help of Holmes Rolston III, who described this condition by saying that the human self "has a semipermeable membrane" of value perception. A person, or "self" in Rolston's words, perceives something of the "natural" value (E_{NV}) of something like the Grand Canyon, and this produces an internal perception of that value, or an "experiential value," (E_{EV}) in the observer (Figure 2.6). Rolston gives an example using a common woodland wildflower, the trillium (*Trillium* spp.), and the experience of enjoying its beauty.

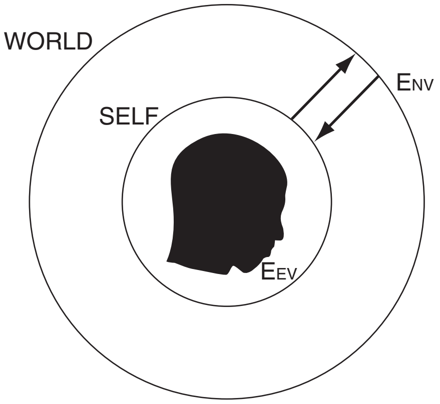


FIGURE 2.6. A schematic illustration of the relationship between the perception of intrinsic value by a human observer and the locus of such value in a natural object. In the diagram, object E possesses a natural or intrinsic value (E_{NV}) which is perceived by a human observer ("self") and internalized as a personal experience of apprehending the value of the object E, an "experienced value" (E_{EV}) of E. (Based on concepts from Rolston 1986. Original drawing by M. J. Bigelow.)

> *...there is some ought-to-be beyond the is, and so the plant grows, repairs itself, reproduces, and defends its kind. If, after enjoying the Trillium in a remote woods, I step around it to let it live on, I agree with this defense, and judge that here is an intrinsic objective value, valued by me, but for what it is in itself.*
>
> (Rolston 1986:111)

The analysis of intrinsic value is presented in a still different way by environmental ethicist Arne Naess, who, upon reading an early handbook on the care and treatment of domestic animals, was amazed to discover that the author spoke passionately about caressing pigs. At one point, the author stated, "Those who have experienced the satisfaction of pigs stroked this way cannot but do it" (Naess 1986). Naess asks the obvious question: how can the author, a human, experience the satisfaction of a pig? The answer, according to Naess, is a simple one. The process that allows us to experience both the satisfaction and worth of a non-human creature is that of *identification*, our tendency to see ourselves in everything alive (Naess 1986). Far from being a sentimental mistake corrected by formal education, Naess asserts that the sense of identification grows stronger as it is informed by knowledge of a creature or an object. Humans, says Naess, "have the capacity of experiencing the intimate relations between organisms and the nonorganic world … the attainment of well rounded human maturity leads to identification with all life forms" (Naess 1986). Naess asserts that identification with non-human life is a virtue developed through the exercise of intellect and habit, and through explicit recognition of the intrinsic value of the other life, or as Regan puts it, "What we see is that humans are necessary to the full realization of the 'goods' of other species. The cheetah's speed is good, but it is not good in itself. It needs to be known by a subject who can know it and take pleasure in it in a sophisticated way. The cheetah does not value his speed in the required way. We can and should. That is the proper spelling out of the notion that every creature has 'a good of its own'" (Regan 1986).

Our combination of experience and perception "let us in on" the presence and qualities of value in a natural object. As a result, our consciousness is able to "share" with the object the qualities of value that were always present in it, but which we now perceive, and to which we respond. As Holmes Rolston III put it memorably, "With every such sharing there comes a caring" (Rolston 1986:104). "All natural science," notes Rolston, "is built on the experience of nature, but this does not entail that its descriptions, its "facts," just are those experiences. Valuing could be a further, nonnuetral way of knowing about the world" (Rolston 1986:104). Regan's, Rolston's and Naess's arguments lead to the conclusion that the ability to perceive the intrinsic value of other species is not only appropriate for humans, but an important distinction of being human.

Most conservation biologists *act* as if they appreciated an intrinsic value of non-human species, and demonstrate it admirably with a career of commitment and a life of personal devotion to the welfare of other creatures. However, if the value inherent in these perceptions is to be shared with others and transformed from personal preference into real "knowledge" about values, it must be expressed in a way that can be understood by others. It is not sufficient for conservation biologists to behave as if non-human species have intrinsic value and hope that everyone else will simply imitate their behavior without asking why. If species truly possess intrinsic value, and if such value should change our behavior toward them, what is the basis of that value, and what is its source?

2.3.2. Ecocentrism as a Basis for the Intrinsic Value

Aldo Leopold was not only the father of the Wilderness Ideal in conservation (Chapter 1), he was also the originator of "the land ethic," an ethical paradigm explaining how humans ought to relate to their non-human environment. As noted in Chapter 1, Leopold came to believe that the land was more than an independent collection of commodities, as he had first been taught in the Yale Forestry School. The land was a system of interdependent processes. The outcome of those processes, when they functioned properly, was sustained production of the commodities associated with them, such as soil, water, timber, wildlife, and forage for wild and domestic animals.

Although Leopold's views were informed by the analysis of science and the experience of conservation management, he realized that an ethical transformation had to take place in both natural resource managers and the public they served. Leopold became convinced that there was not only an efficient and democratic way to manage resources, but a "best" way to manage them. Such management recognized that the system – in Leopold's words, "the land" – had intrinsic value, and included a concept of ethics that recognized this value and worked for the land's health and continued productivity. Without these values, human selfishness and consumptivism would thwart the most informed science and the most enlightened management. Further, Leopold argued, like Emerson, Thoreau, and Muir, that a recognition of the value of the land demanded changes in personal attitudes and behavior – that government conservation policy required the support of personal conservation virtue. Leopold came to believe that the "conservation" of his day, based on nothing but the enlightened self-interest of the Resource-Conservation Ethic, was only a counterfeit that masked the need for the genuine ethical transformation required to change relations between humans and their environment. "I had a bird dog named Gus," Leopold wrote. "When Gus couldn't find pheasants, he worked up an enthusiasm for Sora rails and meadowlarks. This whipped up zeal for unsatisfactory substitutes masked his failure to find the real thing. It assuaged his inner frustration. We conservationists are like that" (Leopold 1966:200). It was this motivation to expose the shallowness of the Resource-Conservation Ethic that drove Leopold to craft a radical alternative.

Leopold was not original in his view that ethics ought to include land and non-human creatures, or that conservation requires private virtue as well as public law. Such concepts are rooted in multiple ethical and religious traditions in a variety of cultures. But Leopold's original contribution was to combine this ethical conservation with practical experience in resource management, and then to inform both with scientific expertise. He wrote, "It is inconceivable to me that an ethical relation to land can exist without love, respect, and admiration for land, and a high regard for its value. By value, I of course mean something far broader than mere economic value; I mean value in the philosophical sense" (Leopold 1966:261). Leopold's writings on the ethical aspects of land management were published after his death as a collection of essays entitled *A Sand County Almanac*. Leopold's land ethic made the ethical treatment of land and resources a central issue in conservation, and a point of serious discussion in academia. His work returned attention to the fundamental question with which John Muir had initiated the great US debate in conservation: What is the best use of nature and natural resources? Leopold's coupling of values (the land ethic) to applied science (game management) began to change fundamental assumptions not only about the best use of natural resources, but also about the nature and purpose of ecological studies. These changes opened the door for the development of a value-driven approach to science and conservation, without which the field of conservation biology could not have emerged.

In his argument for a land ethic, Leopold asserted that it was the land's intrinsic value that led to its "rights." Speaking against those who saw the land only as a repository of "natural resources," Leopold wrote, "A land ethic, of course, cannot prevent the alteration, management, and use of these 'resources,' but it does affirm their right to continued existence, and, at least in spots, their continued existence in a natural state" (Leopold 1966:240). The land ethic assumed the intrinsic value of non-human creatures, even if it did not always articulate the reasons for those assumptions. Like any well-framed ethical system, Leopold's captured the essence of his ethic in a summary moral maxim: "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise" (Leopold 1966:262).

Leopold saw value in every species because each contributed to overall ecological function. Contrasting ecological value to economic value in his own state of Wisconsin, Leopold wrote, "One basic weakness in a conservation system based wholly on economic motives is that most members of the land community have no economic value. Wildflowers and songbirds are examples. Of the 22,000 higher plants and animals native to Wisconsin, it is doubtful whether more than 5% can be sold, fed, eaten, or otherwise put to economic use. Yet these creatures are members of the biotic community, and if (as I believe) its stability depends on its integrity, they are entitled to continuance" (Leopold 1966:246–247). Here Leopold makes two points that environmental ethicists would formalize decades later. First, the intrinsic value of biodiversity should be based on a species' contribution to ecological stability and integrity. Second, such intrinsic value implies a "right to life" of creatures which contribute to that stability and integrity.

These premises, integrated and explicated in later years by others, became the foundations of an ethic known today as ***ecocentrism***, which asserts that the fundamental entity to which both values and rights apply is the biotic community, not individual specimens or species. Leopold argued that the value of a species does not reside in itself, but in its value to the integrity, health, function, and persistence of the community of which it is a part. Callicott rephrased Leopold's original moral maxim of the land ethic in more modern, ecocentric terms as, "A thing is right when it tends to protect the health and integrity of the ecosystem. It is wrong when it tends otherwise" (Callicott 1994a).

Today many conservation biologists see themselves as heirs of Leopold's legacy to restore ethics and value to the science of conservation. As Fiedler et al. (1997:84) put it, "Today the emergence of conservation biology, perceived as a distinct discipline, is a direct result of the failure of resource management fields … to fully embrace the values espoused by Leopold …". Some have argued that Leopold failed to establish an intrinsic value for the land and its components. If species derive value from their usefulness to community function, that is an expression of the ecological usefulness of the species to the community, not of the species' intrinsic value. Some of Leopold's harsher critics have accused him of "ecofascism," making every species subservient to the collective function of the community (Callicott 1999a). Others have noted that the Leopold's concept of the "community" invokes a now discredited view of ecological communities as highly interdependent populations, rather than a view based on more recent research that has demonstrated that most communities are loose associations of independent populations that occur together because of similar environmental tolerances (Callicott 1999b).

Given these objections, many argue that intrinsic value cannot exist apart from a tradition of moral knowledge in which value is imputed to a resource or species by a higher moral authority. Leopold himself acknowledged that a conservation ethic apart from well-grounded philosophical and religious understanding would be incomplete. "No important change in ethics," Leopold stated, "was ever accomplished without an internal change in our intellectual emphasis, loyalties, affections, and convictions. The proof that conservation has not yet touched these foundations of conduct lies in the fact that philosophy and religion have not yet heard of it. In our attempt to make conservation easy, we have made it trivial" (Leopold 1966:246).

The majority of the world's six billion people are "touched [by] these foundations of conduct," drawing their understanding and applications of values, including conservation values, from religious traditions. Such traditions are important in creating and refining a person's individual conservation ethic and, with that, society's ethic. We would trivialize conservation ethics by ignoring Leopold's advice, and the majority of human experience, if we avoided ultimate issues of value that religious traditions and knowledge address. Religious traditions engage the problems and questions inherent in the concept of intrinsic value in comprehensive and diverse ways. They answer some of the most basic and problematic questions of conservation valuation: namely, does intrinsic value exist, what is its source, and how ought we to respond to it?

2.3.3. Intrinsic Value in the Judeo-Christian Tradition

In the nineteenth and early twentieth centuries, conservation developed as a moral movement, undergirded, in part, by a biblical view of the value of the natural world. John Muir argued for the intrinsic value of species because they were "God's creatures" and "part of God's family, unfallen, undepraved, and cared for with the same species of tenderness and love as is bestowed on angels in heaven or saints on earth" (Muir 1916:98).

Despite Muir's legacy, the modern era of conservation did not begin auspiciously in its relations between environmental concerns and the Judeo-Christian tradition. In one of the most influential essays of modern times, The Historical Roots of Our Ecologic Crisis, published in the journal *Science* in 1967, Berkeley historian Lynn White Jr. identified the Judeo-Christian tradition, especially western Christianity, as the cause of the environmental crisis (White 1967). White asserted that in the Judeo-Christian tradition nature had no reason to exist except to serve humans, that Christianity established a dualism of humanity and nature and taught that "it is God's will that man exploit nature for his proper ends" (White 1967:1205). Further, White asserted that "By destroying pagan animism, Christianity made it possible to exploit nature in a mood of indifference to the feelings of natural objects" (White 1967:1205).

White's views were repeated in academic and popular circles throughout the 1970s and became a staple in discussions of ecological ethics in widely used textbooks on ecology during that period (Krebs 1972; Colinvaux 1973; Hinckley 1976). The Judeo-Christian tradition was vilified in all things environmental, from discussions of landscape architecture (McHarg 1969) to pollution and species extinctions (Ehrlich 1971).

Stung by the criticisms of White and others, Christian scholars responded with rebuttals based on careful study and scholarship. Out of that emerged what is today referred to as the ***Judeo-Christian Stewardship Environmental Ethic*** (Callicott 1994a), a perspective that is now one of the dominant worldviews in environmental ethics (Norton 1991), and continues to influence the development of contemporary conservation values.

On the central question of the intrinsic value of species, this ethic speaks without equivocation. In the opening chapter of the Bible's first book, Genesis 1, God repeatedly proclaims that both specific kinds of creatures and natural objects are "good." The goodness acknowledged and perceived by God of his own creation is intrinsic rather than utilitarian because God has no self interests of any kind that could be used to determine the value of the creatures in relation to his own interests. It is equally clear that God has no need of anything and cannot benefit from or be harmed by his creatures in any way (Callicott 1986). But the goodness of the creatures is also intrinsic and non-utilitarian from the human perspective. The repeated pronouncements of creation's goodness are made by God, not humans, and not in any way in relation to humans. Both non-human creatures and humans receive God's blessing to be fruitful and multiply and fill the earth (Genesis 1:22 and Genesis 1:28), but the blessing is given first to non-human species. In this context, environmental ethicist J. Baird Callicott made the following judgement: "The Judeo-Christian Stewardship Environmental Ethic is especially elegant and powerful. It also exquisitely matches the requirements of conservation biology. The Judeo-Christian Stewardship Environmental Ethic confers objective intrinsic value on nature in the clearest and most unambiguous of ways: by divine decree" (Callicott 1994a:36). Although the value of created things can be discovered by humans, that value exists independent of humans and human experience.

Callicott goes on to note that the intrinsic value ("goodness") conferred upon created things is conferred to species ("kinds"), not to individual plants or animals. Humans are free to use individual specimens of living things for their own needs, but are not to destroy the goodness of creation's diversity by eradicating entire species. Were this intrinsic goodness the only value conferred upon non-human creation by the Judeo-Christian tradition, it would be an important contribution. There are, however, many dimensions of biblical teaching that add value to nature. We will note three of particular significance to conservation ethics.

Non-human creatures are appropriate subjects of human care and protection. The concept of active care for creation is explicated in the second chapter of Genesis. "The Lord took the man and put him in the Garden of Eden to till it and to keep it." The verbs rendered as "cultivate" and "keep" are, in most other biblical passages, translated as "serve" (*abad*) and "protect" (*shamar*). The latter is usually translated elsewhere to signify the idea of persistent loving care, as is the case in the biblical passage that says "The Lord bless you and keep (*shamar*) you, the Lord make his face to shine upon you and be gracious to you, may the Lord lift his countenance upon you and give you peace" (Numbers 6:24–26). Both verbs are usually encountered in Scripture as actions that describe service to God, especially as vocation, not as agricultural tasks. They are almost always used in sentences where the subject is a priest or a priestly functionary and the service performed is directed toward God, not toward the object itself or for the benefit of the one performing the service (Walton 2001:185).

An ancient Israelite audience would understand from the text that, in Eden, God had created a "sacred space" and installed the man as its priest. Old Testament scholar John Walton has noted that, in ancient cultures, a priest charged with the care of a sacred space had three primary duties. First, he was to see that the sacred space was kept pure, not defiled or polluted in any way. Second, he was to establish a regular and frequent pattern of worship. Third, he was to monitor the needs of the inhabitants of the sacred space to ensure that they would lack nothing needful (Walton 2001:196). The human presence, as described in Genesis 2:15, is thus presented as one of priestly service to the created world. To discharge this obligation is described here as a fundamental expression of being human. Although White imputed the injunction to "subdue the earth and rule over the creatures" in Genesis 1 as a divine license for oppressive behavior by humans toward creation, most biblical scholars understand these words in light of the specific acts given to humans in Genesis 2. Such a view is more consistent with the biblical ideal of ruling found in both the Old (Deuteronomy 17:14–20) and New Testaments (Matthew 20:25–28, John 13:3–15). The biblical ideal is not oppressive or despotic behavior, but rather one of wise and loving care expressed through acts of service, even costly personal sacrifice. Because it takes the concept of "ruling" seriously, the Judeo-Christian tradition takes human responsibility for the environment seriously. It does not desire that a human become, as Aldo Leopold put it, "plain member and citizen of the biotic community." Instead, it asserts that humans, made in the image of God, have unique responsibilities in the care of creation that they are particularly empowered and authorized to carry out, and for which they will be held personally accountable.

Legal protection is applied to the land as an entity in itself, not as a commodity or as a means of producing a livelihood. In both Exodus and Leviticus, Old Testament books that explicate God's law to his people, God institutes a pattern of rest for the land, a "land Sabbath." "When you enter the land I am going to give you, the land must observe a Sabbath to the Lord" (Leviticus 25:2). God goes on to explain that every seventh year the land shall not be cultivated, but shall receive "a Sabbath rest." The people are admonished not to worry because God will provide sufficient food from the previous year's harvest to ensure a supply until the harvest of the eighth year. Moreover, the land is not to be treated as a commodity at all, but as a personal possession of God. "The land must not be sold permanently, because the land is mine …" (Leviticus 25:23). This concept was reinforced through the practice of "Jubilee." Every 50 years, property acquired by individuals had to be returned to the former owners, so that land could not be accumulated indefinitely as a possession of the wealthy. The Bible treats the land as a moral subject and legal rights are imputed to it (the right of the land to "rest" every 7 years, Leviticus 25:4) and penalties are prescribed for its abuse (Leviticus 26:27–35).

Violation of the land Sabbath is named as one of the reasons foreign adversaries deported the nation of Israel from the land. Speaking of Nebuchadnezzar, the Babylonian king who conquered Judah, the Bible states, "He carried into exile to Babylon the remnant, who escaped from the sword.… Then the land enjoyed its Sabbath rests, all the time of its desolation it rested, until the seventy years were completed in fulfillment of the word of the Lord spoken by Jeremiah" (II Chronicles 36:20–21).

Non-human creation is included in God's stated plans for the redemption of the world to himself. The Judeo-Christian tradition sees the problem of ecological abuse not as isolated acts of selfishness or ignorance, but as rebellion against God (Hosea 4:1–3). Therefore, the solution is not simply better conservation practices, but a reconciliation between the Creator and his creation. The hope and promise of the reconciliation of God, humanity, and creation are described in Old Testament passages such as Isaiah 11 and Hosea 2, and in New Testament epistles like Romans 8 and Colossians 1. The work of conservation and stewardship in the Judeo-Christian tradition is not an isolated concept, but one expression of the greater and more encompassing theme of reconciliation between God, humanity, and the created world. In the Christian tradition, this reconciliation is most vividly represented in the incarnation, in which God becomes part of his creation in the person of Jesus Christ, and through his death reconciles all created things to himself (Colossians 1:15–20). Many conservation biologists identify themselves as Christians, and cite the Bible's message of creation's redemption as warrant for the hope that present efforts in conservation are significant to that future redemption, not futile attempts to save what is already "committed to extinction." Thirty conservation biologists from five continents expressed these ideas to their colleagues in the pages of the journal *Conservation Biology*. Senior author Simon Stuart, Senior Advisor of the Biodiversity Assessment Unit of IUCN, and his co-authors wrote

> *Christians are committed by their biblical beliefs not only to the conviction that God himself cares for his universe in a daily and ongoing way but also that he helps and guides people in their conservation efforts. We are therefore not on our own against the relentless forces of unsustainable development and rapacious materialism. Every time we celebrate a conservation success story such as the recovery of the white rhinoceros in southern Africa, we are strengthened in this present hope that God is working with us to redeem his creation.*
>
> (Stuart et al. 2005:1690–1691)

2.3.4. Other Western Religious Traditions – Islam

Islam arose, as a systematic belief structure, in the seventh century AD in the Middle East, although, like Judaism, it traces its historical ethnic origins through Abraham. Its adherents, Muslims, believe that Allah (God) communicated to humanity through his representative, the prophet Mohammed, whose teachings form the principle distinctions of Islam. Islam, like Judaism and Christianity, offers a monotheistic religious perspective with a theocentric basis. Like Judaism and Christianity, Islam perceives the natural world as a creation of God that reveals his glory and attributes. "The seven heavens and the earth and all therein declare His glory: there is not a thing but celebrates His praise …" (Qur'an' 17:44). Also like Judaism and Christianity, Islam maintains that God is transcendent. Although God values his creation, he is not the same as his creation and is not to be equated with it. God is "totally other," but he fully encompasses his creation and lovingly cares for it. On this point Islam shares with Judaism and Christianity the concept of *immanence* – that God operates within the physical world, always and everywhere intimately present with that world, yet distinct from it. Because God created the world and continues to work within it, the world is not profane, but holy, a place to worship and adore God in any circumstance, therefore "the whole earth is a mosque" (Manzoor 1984). The value of the world originates from God, not humanity.

The intellectual pillars of Islam are *tawhid* (unity), *khilafa* (trusteeship), and *akhirah* (accountability, or, more literally, the hereafter) and form the foundations of its conservation ethic (Hope and Young 1994). From the concept of *tawhid*, Islam perceives religion and science, value and fact, as a unity (Hope and Young 1994; Wersal 1995), making Islam explicit in its opposition to separate the world into divisions of secular and sacred. This perspective makes it natural for Muslims to see the world around them as a creation of God. In such a view they hold a sacramental view of the physical universe where there is no distinction between religious and secular law, nor any concept akin to "the separation of church and state" that characterizes western cultures. Thus, conservation law must be grounded in Islamic law. Further, an important purpose of religious teaching is to provide independent judgment, correction, and regulation of scientific activity. Many Islamic scholars and scientists are critical of western science because they see its separation from religious tradition as the cause of its abuses. As Islamic scientist Seyyed Hossein Nasr put it, "Western science has become illegitimate because scientists and the rest of society fail to see the need for a higher knowledge into which it could be integrated. The spiritual value of nature is destroyed. We can't save the natural world except by rediscovering the sacred in nature" (Hope and Young 1994).

Islam sees nature as teleological, harmonious, and dependent. Because such traits represent its original state and God's continued intention for it, Islamic belief supports an attitude of moral obligation in regard to human interaction with nature. The human role is one of *khalifa* (trustee) and the human duty is to maintain the appropriate purpose, harmony, and dependence that Allah imputed to natural systems. The concept Judeo-Christian thought would describe as "stewardship" is referred to in Islam as "viceregency" (Zaidi 1991:41). In the words of the Qur'an', "Behold, the Lord said to the angels: 'I will create a viceregent on earth …" (Qur'an' 2:30).

The third pillar, *akhirah*, arises from the Islamic view of the physical world as a testing ground of human character. Faithful stewardship is one criterion by which God determines the faithfulness of humankind to him, and from this, decides a person's eternal destiny. Because there is no division of sacred and secular, eternal destiny is enforced and exemplified in present circumstances. Under Islamic law, if one ceases to manage land responsibly, one can lose ownership of the land. Land, water, air, fire, forests, sunlight, and other resources are considered common property, not merely of humans but of all living creatures (Masri 1992). Expression of these principles, in the context of conservation can be studied in detail in a recent comprehensive summary and systematic arrangement of Islamic teachings on stewardship, *The Islamic Principles for the Conservation of the Natural Environment*, a work produced through the collaborative efforts of a number of modern Saudi scholars (Callicott 1994a).

2.3.5. Eastern Religious Traditions and Conservation – Hinduism and Buddhism

2.3.5.1. Hinduism

Hindus believe that at the core of all being is one reality, but not a "God" in an Islamic, Jewish, or Christian sense of a transcendent, supreme being existing independently of other beings that are his own creations. Rather, in Hinduism all things that appear as individual entities are reflections and manifestations of the one essential being or *Brahman*. One of the sacred writings of Hinduism, the *Bhagavadgītā*, states that the Supreme Being "resides in everywhere" (Chapter 13, verse 13). In this view the Hindu perception of nature is best understood as *prakrti*, the matrix of the material creation. *Prakrti* is seen as the expression of the supreme intelligence and physical form of Brahman. Hindu scholars and teachers often refer to Brahman metaphorically as a tree, with its roots "above," in the spiritual dimension, and its branches "below," in the physical world. The branches of Brahman are conceived as five fundamental elements of *prakrti*; sky (space), air, fire, water and earth. Before every Hindu worship service, the five elements are purified within the worshippers and in the external environment in which the service takes place. Flowers are offered as purification for the sky, incense for the air, light for fire, water for water, and fragrance for the earth. It is therefore natural for Hindus to view nature as something internal rather than external, neither alien nor hostile, but inseparable from human identity and existence (Rao 2000).

To the Hindu, every act, willfully performed, leaves a consequence in its wake because human life and action are inseparable from their environment. This is the Hindu concept of *karma*, from the Hindi root *kr*, "to do." Karma has a general connotation of "action," but is more broadly interpreted as the belief that every human action creates its own chain of reactions and events that will always be with that person, and creates inescapable consequences that must be faced (Dwivedi 2000). As stated in another sacred writing of Hinduism, the *Mahābhāratā*, "an action, which has been committed by a human being in this life, follows him again and again (whether he wishes it or not)" (quoted in Dwivedi 2000:15). Attaining an ideal life depends on choosing right actions and living within an ethos, or set of duties (*dharma*) that produce good consequences (good karma), supported by a purity and balance of the five basic elements within and around a person. The goal is a life harmonious with nature by creating an environment free of pollution, for polluted elements make the human body subject to disease and distortion, no longer an appropriate expression of Brahman. Similarly, the protection of cattle by Hindus is an expression of the belief that humans are responsible for the care of non-human creatures (Rao 2000). And because of Hinduism's doctrine of birth and rebirth (reincarnation), Hinduism requires not simply respect for other creatures, but reverence, for, in Hindu writings, even the Supreme Being takes on various incarnations as a fish, a tortoise, and a boar, among others (Dwivedi 2000). The duties warranted by these beliefs are stated in Hindu writings, such as Prthivi Sūkta, a hymn devoted to praise of Mother Earth, as explicit duties. In this hymn, the worshipper makes this request,

> *O, our Mother Earth! Sacred are thy hills, snowy mountains, and deep forests. Be kind to us and bestow upon us happiness. May you be fertile, arable, and nourisher of all.*
>
> (quoted in Dwivedi 2000:10)

Hinduism has had a long and significant influence on ecology and conservation. Two of the earliest and most influential writers in US conservation, Ralph Waldo Emerson and Henry David Thoreau (Chapter 1), were influenced by Hinduism in their perception and understanding of nature. Hinduism's teaching that all beings are an expression of the one essential being leads to a sense of identity between humans and other living things. Non-human species and non-living objects are seen as manifestations of one's own life, and are therefore to be protected and preserved. Hinduism is an important component of eco-philosophies such as "Deep Ecology" because it strongly identifies humans with other species and natural objects (Naess 1989). More than any other religious tradition, Hinduism explicitly supports identification with non-human life as a genuine perception of reality and a basis for the care of non-human creatures.

2.3.5.2. Buddhism

Buddhism is an agnostic religion, recognizing no deity. Buddhism focuses on mastery of self and integration of the self with one's surroundings through direct knowledge, discriminating awareness, and deep compassion (Kaza 1990). But Buddhism also has been called as the world's most eco-centric religion (Sponsel and Natadecha-Sponsel 1993) because, for the Buddhist, "an environmental ethic becomes a practice in recognizing and supporting relationships with all beings" (Kaza 1990:24).

The fundamental axiom in Buddhism is the Law of Dependent Co-Arising, a formalization of the concept that all events and beings are interdependent and interrelated (Kalupahana 1987). In the words of its own sacred writings,

> *For one who truly sees the pure and simple arising of phenomena and the pure and simple continuity of conditioned things, there is no fear. When with wisdom one sees the world as just like grass and wood, not finding any selfishness, one does not grieve with the idea, 'this is not mine'.*
>
> (quoted in Batchelor 1992:10)

On the basis of this law, Buddhism stresses a unity of self and environment. The Buddhist ideal of *nirvana*, the awakening into a state of bliss, is reached when the boundary separating the self from its surroundings and all mortal cravings is extinguished (Smith 1958). Therefore, in the context of conservation, Buddhism does not emphasize that resources are limited, but that a person should limit his use of resources.

Buddhism asserts that the foundation of knowledge is personal experience. Experiential knowledge is especially emphasized in spiritual matters, so personal meditation is accorded high value, as are natural environments conducive to such meditation. Buddhism teaches respect and compassion for all life, and values undisturbed natural environments as "sacred space" for meditation (Brockelman 1987; Buri 1989). Buddhism's goal is increasing self-knowledge, with increasing self-mastery and self-restraint. Its "Middle Way" of correct moral behavior emphasizes detachment from material things and present concerns. Buddhism takes a high view of personal responsibility because it shares, with Hinduism, the doctrine of karma. Future happiness results from appropriate present conduct. Wrong actions of the past will produce bad effects in the present, so Buddhism encourages environmental education and appropriate environmental behavior, not simply for present consequences, but for future ones.

2.3.6. Practical Implications – Faith-Based Organizations in Conservation

2.3.6.1. *"Goal Rational" Versus "Value Rational" Conservation*

In their widely read paper, "The Death of Environmentalism," authors Michael Shellenberger and Ted Nordhaus assert "What the environmental movement needs more than anything else right now is to take a collective step back to re-think everything. We will never be able to turn things around as long as we understand our failures as essentially tactical and make proposals that are essentially technical" (Shellenberger and Nordhaus 2004). The problem Shellenberger and Nordhaus describe is considered by many to be the fruit of a "goal-rational" perspective that has historically supported traditional environmental agencies and NGOs, a view in which measurable ends, achieved by technical means, serve as the index of conservation success (Abuyuan 2006). However, such an approach, even if successful, may do nothing to actually enhance the public's dedication to conservation or its respect for nature because it does not address public motivation or private practice. As environmentalist David Orr has noted, conservation biologists "lack both a deep explanation of what ails us and a larger cosmology that resonates with the public" (Orr 2005). Goal-rational approaches emphasize technical competency but fail to frame conservation as moral endeavor. Without a moral framework, most individuals outside the scientific community fail to perceive moral value in the conservation effort, even when the effort achieves "success." The problem is increasingly attracting the attention of environmental ethicists, like Kyle Van Houtan, who ask "On what basis can conservation achieve widespread cultural legitimacy? What are the particular currencies for a conservation ethic?… Whoever carries the responsibility for doing ethics … a stark reality confronts them. The ecological crisis is ever increasing and the voting public does not seem to care.… No environmental ethic is articulating and motivating lifestyle changes that are both significant and widespread" (Van Houtan 2006:1369).

All major world religions possess teachings about creation and nature, along with sophisticated insights into the relationship between human beings and their environment. Such insights can lead to motivation for environmental stewardship that is viewed with widespread cultural legitimacy (Abuyuan 2006). Today religiously-based insights about conservation are being applied in faith-based organizations (***FBOs***) throughout the world. An understanding of their growing impact in conservation (Abuyuan 2006) is relevant and vital to an understanding of the modern world conservation effort.

2.3.6.2. *Jewish and Christian FBOs*

In September of 1989 the Jewish Theological Seminary of America devoted its High Holiday message, published as a full-page ad in the New York Times, to the environmental crisis (Schorsch 1992). In 1991, Jews and Catholic Christians collaborated with the Institute for Theological Encounter with Science and Technology (ITEST) to sponsor the symposium and workshop, "Some Christian and Jewish Perspectives on the Creation" which included significant discussion and subsequent publication of Jewish and Christian expositions of biblical teaching on creation stewardship (Brungs and Postiglione 1991). Subsequently, the formation of the Coalition on Environment and Jewish Life (COEJL) in 1993 has taken an even more active role in conservation and environmental stewardship. As part of its efforts, COEJL has formed an Environmental Leadership Institute, produced a comprehensive Environmental Policy Platform, a program for "Greening Synagogues," developed an umbrella organization, the Jewish Global Environmental Network, and organized an extensive array of environmental education programs for students of all ages (www.coejl.org). In 2005, COEJL helped to form and initiate the Jewish Global Environmental Network (JGEN), which began work to develop partnerships and collaborative initiatives through which Jewish environmental leaders in Israel and around the world could work together for a sustainable future.

The array of Jewish and Christian conservation efforts is too numerous to recount here, but can be represented by some notable examples. Umbrella organizations and networking groups have become necessary to list, and attempt to coordinate, the wide variety of Jewish and Christian FBOs now active in conservation. Among these are The National Religious Partnership for the Environment (NRPE), established in 1993, which includes leadership from the National Council of Churches, the US Catholic Conference, the Coalition on the Environment and Jewish Life, and the

Evangelical Environmental Network. The NRPE's goal is to increase engagement in environmental stewardship by local congregations as well as to demonstrate and address connections between environmental concerns and social justice. Similarly, the Evangelical Environmental Network (EEN) was formed in 1993 through a cooperative effort of World Vision and Evangelicals for Social Action (ESA) for a similar purpose. In addition to these and other organizations, individual denominations have engaged in a variety of activities to promote environmental policies based on a biblical understanding of the stewardship of creation (e.g. Guenthner 1995).

The Christian FBO most actively engaged in conservation policy, management, and research is A Rocha International (ARI). Initiated in Portugal in 1983, ARI now coordinates the activities of 17 national chapters on 5 continents. It is the only conservation FBO with member status in the World Conservation Union (IUCN), and its membership is warranted by significant successes in conservation, even in very difficult circumstances. In the politically unstable climate of Lebanon, ARI has been successful in preserving one of the last major wetland areas in the Near East land bridge between Europe and Asia, the Aamique Wetland. A major stopover for hundreds on species migrating between Eurasia and Africa, ARI's efforts combine scientific study (including bird surveys now containing over 29,000 records with 8 new species records for Lebanon), an environmental education program for local schools, a community arts program for women, and a summer science club for local students. A Rocha – Kenya has worked effectively with local residents and government officials in the Arabuko-Sokoke Forest, the largest remnant of dry coastal forest in East Africa. Here they have developed the Arabuko-Sokoke Schools and Eco-Tourism Scheme (ASSETS) to establish community involvement in local conservation. In this effort, A Rocha – Kenya developed facilities and services for tourists who come to see the forest's noteworthy plant and animal life, then diverts the funds generated to provide scholarships for local school children ("eco-bursaries") and to nature conservation. Proposals for Natura 2000 status for Portugal's Alvor Estuary stem directly from A Rocha – Portugal studies in that country. In the UK, the once derelict Minet Site in Middlesex is being transformed into a county park and conservation area by A Rocha's UK chapter. Worldwide, A Rocha has been involved in efforts with other conservation organizations in the study, management, and conservation of 42 species of plants, invertebrates, reptiles, amphibians, fish, birds, and mammals (www.arocha.org).

2.3.6.3. *FBOs in Islam*

In Islam, concerns in conservation are increasingly well-represented and put to practical application by the Islamic Foundation for Ecology and Environmental Sciences (IFEES). Established in the mid-1980s, IFEES has grown in membership and influence to become the most widely recognized international Muslim conservation organization, not only articulating the Muslim understanding of conservation and environmental stewardship, but working out such understanding in practical applications. Their efforts in research, teaching, and training have reached the Muslim community throughout the world, with active or developing projects in eight countries on three continents (Asia, Africa, and South America). In Yemen, for example, IFEES has initiated the rehabilitation of traditional water conservation practices through the application of Islamic conservation principles (www.ifees.org). IFEES also contributes as a consultant to such international conservation agencies as The World Wide Fund for Nature and the Earth Charter Consultative Committee. A still more recently established Islamic FBO, the African Muslim Environmental Network (AMEN) (www.arcworld.org/news.asp?pageID=71) was formed in 2005. Among other efforts, AMEN has been active in coordinating the revival of traditional and sustainable fishing practices in Muslim communities along the East African coast, and in establishing a program of forest protection in the same region based on guidelines of Islamic law.

2.3.6.4. *Conservation Activism in Hinduism*

There is a tension between environmental conservation and Hinduism that, in some ways, parallels the tension Lynn White Jr. alleged between conservation and Christianity. Hinduism has been criticized in the context of ecology and conservation by many scholars because it teaches that the physical world and its diverse entities are derivatives of the undifferentiated and unmanifest Brahman, the supreme reality. The physical world is therefore "less real," less significant and liable to be dismissed or even denigrated by devout Hindus seeking higher and greater spiritual realities (Chapple 2000). Callicott, for example, claimed that Hinduism teaches that "the empirical world is both unimportant, because it is not ultimately real, and contemptible, because it seduces the soul into crediting appearances, pursuing false ends, and thus earning bad *Karma*" (Callicott 1994b). However, the expression of Hinduism in ecological context does not support this criticism. Although it is difficult to name an exclusively Hindu conservation organization, Hinduism has engaged itself forcefully and practically in the conservation of biodiversity. The most famous expression of such engagement is the *chipko* movement of northern India. *Chipko* is derived from a Hindi word meaning "to hug," or "to embrace." The movement is dated from a protest near the town of Gopeshwar in the province of Uttar Pradesh in 1973. Villagers, protesting logging policies, went into the forests and physically embraced trees to be cut by loggers. The loggers, unwilling to harm the villagers, did not cut the trees.

What followed this initial protest was a long and complex struggle over government forest and development practices which continues to this day. The motivations behind the *chipko* movement were not inspired exclusively by religious conviction. They also were motivated by political issues of self governance (the right of the villagers rather than the government to determine the fate of local forests) by issues of social justice (the government had denied the villagers a permit to cut trees to make farm implements, but had granted a request in the same forest for a foreign company to cut trees to make sporting goods), and by concerns for local environmental quality (the increase of soil erosion to the detriment of local agriculture and water quality) (James 2000). But they were also inspired by the widespread beliefs of ordinary Hindus that trees were sacred objects. The forest, in local Hindu folk teaching, is seen as the highest expression of the earth's fertility and productivity, personified by the goddess Vāna Durgā, the tree goddess and earth mother (Shiva 1989). Most of the protesters were, initially, women, and they gave the *chipko* movement its most dramatic confrontation and its most memorable slogan. In a protest in 1977, a forest officer of the Indian government went into the forests to convince the women that the proposed logging was scientifically sound and economically indispensable. He ended by saying, "You foolish women! Do you know what the forests bear? Resin, timber, and foreign exchange!" But, not intimidated, the women hurled the question back at the forest officer with a very different answer. "What do the forests bear?" they cried. "Soil, water, and pure air! Soil, water, and pure air sustain the earth and all she bears!" (James 2000).

The complexities of the *chipko* movement must not be oversimplified, but it does demonstrate how religious values affect social and political events that shape the outcomes of conservation. In one sense, Callicott's criticism proved correct. The *chipko* movement did include an element of negating the world, however, it was not the natural world that was negated in its protests, but rather the world of scientific and economic reductionism that made natural objects worth no more than their value as market goods.

2.3.6.5. Conservation FBOs in Buddhism

An expression of the conservation values of Buddhism is modeled in current conservation efforts led by many of Buddhism's most well known and influential authorities. The Dalai Lama of Tibet, perhaps the world's foremost Buddhist leader, is also one of the world religious community's foremost conservationists. With his support, the Buddhist Perception of Nature Project (begun in 1985), sponsored financially by the World Wildlife Fund, identified and integrated environmentally relevant passages from Buddhist scriptures and secondary literature. In Thailand, the Buddhist leader Chatsumarn Kabilsingh contributed to this project by framing Buddhist doctrines into "teaching stories" that have been distributed and used in environmental and conservation education curricula in Buddhist cultures throughout southeast Asia (Kabilsingh 1990). Many of these stories emphasize Buddhist instruction to not cause harm to others in one's environment and to protect natural objects such as trees, rivers, and animals (Kaza 1993). Also in Thailand, the Buddhist monk Pongsak Tejadhammo established the Dhammanaat Foundation in 1985 to preserve forests and create greater environmental harmony and security for local villagers. The foundation is not merely a preserve, but is also a site of ecological restoration (Sponsel and Natadecha-Sponsel 1993). Throughout Thailand, Buddhist monks have adopted a strategy of forest protection by ritually ordaining individual trees and wrapping them in sacred orange robes normally worn only by monks. A devout Buddhist would never kill a monk, so the symbolism is obvious in its cultural context. The Buddhist Peace Fellowship, founded in 1978 to address peace and environmental issues, is yet another example of systematic attempts by Buddhists to contribute constructively to worldwide conservation efforts.

Perhaps most influential in conservation is the Buddhist organization Tzu Chi (www.tzuchi.org/global/services/environ.html). Although a broad-based relief and development organization with varied interests and ministries, Tzu Chi is actively engaged in environmental protection, particularly in southeast Asia. Among its over five million members worldwide, 45,000 are registered as "environmental protection volunteers." Many of Tzu Chi's efforts have been directed at environmental education, and at recycling efforts. Their paper recycling alone is estimated to have supplied paper equivalent to what could have been harvested from 360,000 20-year-old trees. Tzu Chi's founder, Master Cheng Yen, teaches that "we should keep forests in good condition. We should not cut down too many trees, nor should we pump underground water without limit or steal sand and rocks from nature" (www.tzuchi.org/global/services/environ.html). Consistent with this practice, the organization has designed a reusable bag, available to members and non-members, in which one can carry a bowl, cup, and chopsticks to minimize the use of disposable eating utensils in markets and restaurants.

2.3.6.6. Future Roles and Contributions of FBOs in Global Conservation

Conservation FBOs have proven capable of effective, productive partnerships with secular organizations and agencies, and their influence is growing. Today many conservation and development organizations have a person, or in some cases entire departments and programs, assigned exclusively to working with faith-based communities and FBOs. On example is the Faith and Environment Program at The World Bank, led by Tony Whitten.

In commenting on the role of FBOs in conservation and the need for conservation NGOs to work with them, Whitten remarked, "I ask them (skeptics) why on Earth they wouldn't (engage FBOs)? Why would they avoid working with these NGOs when they're available? When they reach people so easily, when their agendas coincide – what on Earth could be the reason for not doing it?" (quoted in Abuyuan 2006:221).Because conservation FBOs provide opportunity for people to transform faith commitments into meaningful action, faith-based organizations engaged in conservation inspire high levels of loyalty and commitment among their staff, volunteers, and constituency, significant, meaningful connection with local communities, and profound ethical motivation for their conservation work. As environmental ethicist Kyle Van Houtan noted, "To succeed as a social cause conservation needs a hope that academic science itself cannot provide. Conservation needs a cultural legitimacy that inspires enthusiasm, allegiance, and personal sacrifice – in other words, actual changes in human behavior" (Van Houtan 2006:1371). Conservation FBOs contribute to relating conservation ideals to the changes in human behavior that Van Houtan refers to. But to make this connection, a discussion of conservation ethics must move beyond a discussion of theoretical values to the actual practice of behaviors that advance conservation in everyday life, practices which might be best described as *conservation virtues*. Recognizing the value of working with faith-based communities and FBOs, Conservation International's (CI) Faith-based Initiative Program is actively engaged with religious leaders and faith-based communities throughout the world, not only to achieve short-term conservation goals, but to work together with such communities in ways that embed conservation in belief structures and motivations that have enduring cultural legitimacy. In China's Sichuan Province, for example, Tibetan Buddhist monks work with CI to help protect the mountains, forests, and lakes. The monks patrol in areas designated sacred by their monasteries, helping to prevent hunting and regulate herb collection. In Colombia, CI has partnered with the Catholic Church to protect the Critically Endangered yellow-eared parrot (*Ognorhynchus icterotis*) and the Quindío wax palm (*Ceroxylon quindiuense*). Used for centuries in Palm Sunday mass ceremonies, the palm was being over-harvested, in turn threatening the parrot, which depends on the palm tree as its sole habitat. In Indonesia, CI has partnered with Hindu religious leaders to protect rare and threatened sea turtles. In this effort, CI worked with Hindu priests to ban the use of turtle meat in religious ceremonies, drawing on beliefs that call for restraint in overuse of nature. Also in Indonesia, CI has worked with Islamic scholars to help adapt a traditional land management system called "Hima," which is drawn from the sacred Islamic texts, toward goals of biodiversity conservation (Conservation International 2007).

2.4. The Problem of Practice: Do Conservation Values Require Conservation Virtues?

2.4.1. The Problem of Plastic Trees

In 1972, the city of Los Angeles, California (USA) made an innovative proposal for urban beautification. It planned to line the median strip of a major boulevard with plastic trees. The installation of a new box culvert along the strip has not left sufficient soil for real trees to grow, so in their place, city planners proposed the addition of plastic trees constructed of factory-made "leaves" and "branches" wired to plumbing pipes. The trees were "planted" in aggregate rock coated with epoxy, and after their installation, an unknown person or persons added plastic birds (Tribe 1974). Despite the unnaturalness of plastic trees, proponents of the plan could marshal a compelling argument: only plastic trees, they reasoned, could survive the soil-deficient, smog-ridden environment of downtown Los Angeles, and a plastic tree, however artificial, would be more appealing to aesthetic values of people than a dead or dying real tree. Evaluating the problem of plastic trees from the standpoint of cost–benefit analysis, urban research planner Martin Krieger concluded that "the demand for rare environments is a learned one" and "conscious public choice can manipulate this learning so the environments which people learn to use and want reflect environments that are likely to be available at low cost.… Much more can be done with plastic trees and the like to give most people the feeling that they are experiencing nature" (Krieger 1973).

In these remarks, Krieger, perhaps unintentionally, has succinctly defined a fundamental question to be answered in all debates about the value of natural objects and environments. Namely, is the goal to determine the value of a creature – such as a tree – or a natural object – such as a cavern like the Cathedral in the Desert – or is the goal to teach people to use and want environments that can be made available to them easily and cheaply? In other words, do we address and determine the true value of diversity and rarity, or do we teach people not to miss them when they are gone?

Every attempt to determine the value of resources and species begins with assumptions related to our stance on these questions. For example, in recreation science, the concept of "user satisfaction," noted earlier in this chapter, is a common measure of the value of landscape and biotic resources associated with outdoor recreational experiences, based on human levels of satisfaction, expectations, and preferences. In a study of user satisfaction in the Apostle Island National Lakeshore in Wisconsin (USA), Dustin and McAvoy (1982) reported "people appear to be growing less sensitive to the environmental degradation that inevitably accompanies crowding … as use levels increased, recent visitors became more tolerant of environmental degradation." Such findings make Leopold's words about wilderness disturbingly prophetic: "Perhaps our grandsons, having never seen a wild river, will never miss the chance to set a canoe in singing waters" (Leopold 1966:116).

POINTS OF ENGAGEMENT – QUESTION 2

Conservation biologists have rejected Krieger's vision of providing "environments that people use and want at low cost" as a fundamental objective of their work. Why was this vision of "environmental management" rejected and what alternative visions have replaced it? What do the alternatives reveal about what conservation biologists value?

2.4.2. From Values to Virtues: Virtue-Based Ethics in Conservation

The legal ethicist Lawrence Tribe, responding to Martin Krieger's rationale for using plastic trees noted, "Policy analysts typically operate within a social, political, and intellectual tradition that regards the satisfaction of individual human wants as the only defensible measure of the good, a tradition that perceives the only legitimate task of reason to be that of consistently identifying and then serving individual appetite, preference, or desire" (Tribe 1974:1325). These words should profoundly disturb students of conservation biology, especially when we consider how much of the discipline's efforts in value determination are based solely on human appetite, preference, and desire.

Although humans perceive intrinsic and aesthetic values in other species and natural objects, human appetites and preferences cannot be the ultimate foundation of value. In such a system the sovereignty of wants becomes the tyranny of whims. It is only when we link values to purposes greater than self-interest that such values become more than expressions of personal preference. As Tribe puts it, "By treating human need and desire as the ultimate frame of reference, and by assuming that human goals and ends must be taken as externally given, … rather than generated by reason, environmental policy makes a value judgment of enormous significance. And, once that judgment has been made, any claim for the continued existence of threatened wilderness areas or endangered species must rest on the identification of human wants and needs which would be jeopardized by a disputed development" (Tribe 1974:1326).

Tribe's point is that we must decide whether our obligation is to satisfy our desires or to preserve what is valuable, independent of those desires. "We can be truly free to pursue our ends," notes Tribe, "only if we act out of obligation, the seeming antithesis of freedom. To be free is not simply to follow our ever-changing wants wherever they might lead. To be free is to choose what we shall want, what we shall value, and therefore what we shall be" (Tribe 1974:1326–1327). As in all other things, values in conservation biology must mature into ethics that govern behavior if those values would be meaningful. Ethics that address behavior can be grouped in three categorical systems.

Ethics of ***teleology*** focus on attention to outcomes and consequences of behavior. Conservation employs ethics of teleology when its arguments focus on the economic values of individual species or total biodiversity, the market value of ecosystem services, or the monetary values of biotic resources like timber or game.

Ethics of ***deontology*** focus on rules and obligations. Conservation employs arguments of deontology when it addresses our debt to future generations, our need to obey conservation laws, or our duty to respect religious traditions that stress obligations to God, to other people, or to non-human life and inanimate objects as manifestations of God's creation that have been placed in our care.

Ethics of ***areteology*** focus on personal virtue. The central claim of areteology is that certain traits of character (virtues) are essential for correct ethical behavior. To paraphrase Aristotle, virtue is a state of praiseworthy character, developed over time, made perfect by habit (Bouma-Prediger 1998). Areteology addresses significant issues and, perhaps more importantly, patterns of behavior that affect conservation practice. The development of virtue-based environmental ethics is today an emerging contribution with a radically different approach to ethical dilemmas in conservation.

2.4.3. What are Appropriate Conservation Virtues?

In virtue-based ethics, correct behavior is not a fulfillment of an obligation or submission to a rule, nor is it an action taken to achieve a desired material outcome. Rather, ethics of areteology view ideal behavior as the habitual pursuit of excellence toward a moral idea. Areteology asserts that we are what we do. We become brave by choosing to act bravely. We become just by practicing acts of justice. And we become true conservationists and stewards by caring for and preserving species and biodiversity. Ethicist Steven Bouma-Prediger makes the radical assertion that certain traits of character are essential to the "care of creation." These traits include (1) *receptivity and respect* to be able to acknowledge the integrity and interdependence of the non-human world and to be able to perceive and appreciate the value of biodiversity; (2) *self-restraint and frugality* to appreciate the limits of creation and not damage its vitality or productivity; (3) *humility and honesty* to have a proper estimate of our human abilities and their limits and the refusal to deceive ourselves about what those limits are;

(4) *wisdom and hope* to appreciate the fruitfulness of the biological world, enjoy its legitimate pleasures, and confidently expect its future good; (5) *patience and serenity* to be able to allow both ourselves and other creatures to experience Sabbath (rest), either in a time of ceasing from labor or ceasing from taking things from creation and making it labor; (6) *benevolence*, *and love* to have the motivation to work for the good of other creatures and empathize with their needs and hardships in a world dominated by the human species.

Areteology contributes an essential principle for application of conservation values and ethics in all cultural and religious contexts, namely that it is not sufficient for conservation biologists to simply assert that a particular slate of values is compatible with conservation goals. They also must practice habits of behavior and qualities of character which contribute to and are consistent with the work of biodiversity conservation. Such habits and qualities are necessary not only to make the values of conservation biology persuasive to others, but are essential to every conservation biologist who desires to appreciate and enjoy the values that conservation biology promotes.

The idea that conservation requires habits of virtue, not merely choices of values, is rooted in the writings of early US conservationists such as Emerson, Thoreau, and Muir. Speaking of the deficiencies of the "conservation" of his own day, Aldo Leopold wrote, "It defines no right or wrong, assigns no obligation, calls for no sacrifice, implies no change in the current philosophy of values. In respect of land-use, it urges only enlightened self-interest" (Leopold 1966:244). Leopold consummated his point with an allusion to the biblical story of Satan tempting Jesus to turn stones into bread to satisfy his hunger. "In our attempt to make conservation easy," Leopold asserted, "we have made it trivial. When the logic of history hungers for bread and we hand out a stone, we are at pains to explain how much the stone resembles bread" (Leopold 1966:246).

Thus, we come full circle. The primacy of virtue, espoused by philosophers like Aquinas and Kant, practiced in conservation by Thoreau and Muir, and articulated in the land ethic of Leopold, is required to supplement what science alone cannot provide. Unless people cultivate the practice of conservation virtue as well as the observance of conservation law, conservation is likely to remain a frustrated and limited enterprise. We can see why as we close this chapter with a case history of conservation from Indonesia.

2.5. Orphaned Orangutans: Ethical Applications in Conservation

The orangutan (*Pongo pygmaeus*) and Sumatran oran gutan (*Pongo abelii*) are arboreal, forest-dwelling great apes whose populations are now restricted to the islands of Borneo and Sumatra. In 2006, the IUCN listed the orangutan as endangered, and the Sumatran orangutan as critically endangered. Infant orangutans bring high prices in the pet trade, creating strong motivation among local people to capture them by first killing their mothers, and then taking the infant to market (Figure 2.7). In Indonesia, where most of the world's orangutan population resides, such practices are unlawful, but nevertheless common, because laws against such actions are not consistently enforced, and profits are high. Some can make as much money from the sale of one infant orangutan as from a year of local employment.

Enforcement officers arrest some traders, but that only solves half the problem. Orangutans spend at least 7–8 years with their mothers before becoming independent. Thus, orphaned orangutans lack the skills to live in the forest alone. The Indonesian government lacks the resources to "rehabilitate" orphaned orangutans that are taken out of the pet trade, but some private conservation organizations, such as the Orangutan Conservancy (OC), have taken up the responsibility of helping to fund this kind of work.

OC was started by individuals moved with compassion over the plight of orphaned orangutans, which number in

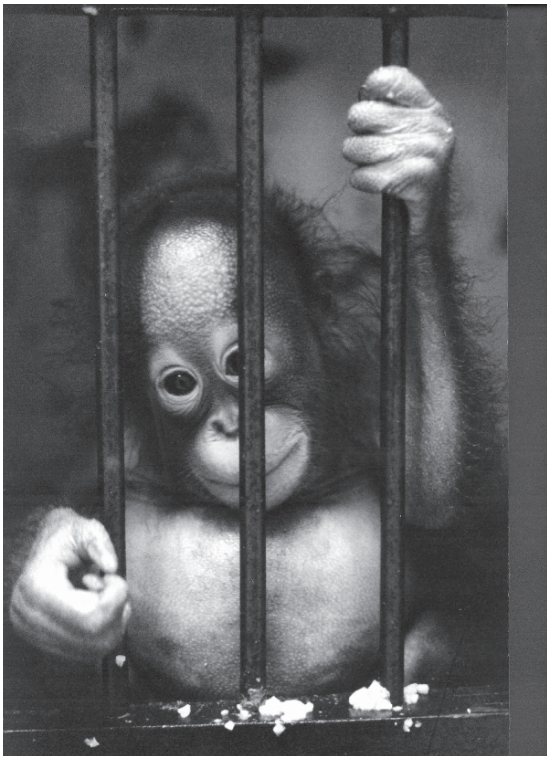


FIGURE 2.7. A caged infant orangutan (*Pongo pygmaeus*) awaits sale in a pet market in Indonesia. Although illegal, such trade in infant orangutans is common because profits from sales are high and laws against such trade are not consistently enforced. (Photo courtesy of Anne E. Russon and Orangutan Conservancy.)

Figure 2.8. At the Orangutan Conservancy's Nyaru Menteng Orangutan Rehabilitation Center in Indonesia's Kalimantan province local Indonesian women serve as nurses and medical technicians to nurse infant organgutans rescued from the pet trade back to health through proper medication, socialization, and diet. The Conservancy's ultimate goal is to rehabilitate the orphaned orangutans by teaching them food gathering, predator avoidance, and social interaction skills that will permit them to live independently in the forest. If successful, the effort could potentially add thousands of orangutans to the wild population. (Photo courtesy of Sarita Siegel and Orangutan Conservancy.)

the hundreds each year. Many became aware of the problem through the efforts of Dr. Willie Smits, the founder of one major orangutan reintroduction project, who originally had come to Indonesia to study tropical forest fungi. Smits found an infant female orangutan in a garbage can. He discovered, on closer inspection, that the orangutan was still alive. In the process of nursing her back to health in his home, Smits became involved with the growing and widespread problem of orphaned orangutans.

In collaboration with Smits and Lone Droscher-Nielsen, a former flight attendant from Denmark who began learning about the orangutan problem through her visits to and volunteer work in Indonesia, conservation scientists, veterinarians, local Indonesians and foreigners from all walks of life have organized to establish and support rehabilitation centers whose goal and curricula are to return orphaned orangutans to wild environments. Among these projects, the largest one supported by the OC is the Nyaru Menteng Orangutan Rehabilitation Center in Indonesia's Kalimantan province. Here infant orangutans rescued from the pet trade are first nursed back to health with proper diet and medical attention (Figure 2.8), and then socialized with other orangutans and helped to acquire forest knowledge and skills. In a nursery and "baby forest," they begin to learn the foraging, nesting, arboreal locomotion, predator avoidance, and other skills needed for their natural lifestyle. Orangutans from 2½–5 years old are moved to "Midway House" where, in a forest, they progress to learning advanced arboreal and foraging skills in a larger natural environment. At Midway House, Lone and her co-workers also teach the young orangutans how to avoid dangers like venomous snakes. Orangutans over 5 years old that successfully complete their training at Midway House are moved to one of three preselected forested islands where they begin to live semi-independently. The final step, not yet completed, is to release rehabilitated orangutans to a mainland expanse of protected forest (www.orangutan.com). There is considerable pressure to move forward with the final step because of the growing intensity of the problem. The facilities at Nyaru Menteng, originally designed to care for 200 orangutans, are currently holding over 700.

The growing problem of orphaned orangutans illustrates both the complex nature and practical role of ethics and values in the work of conservation biology, and the interaction of ethics and values with science, economics, law, and culture. In every step of this example, opposing forces of motive and restraint interact to either make progress toward a solution or further exacerbate the problem (Figure 2.9). Initially, economic considerations are the motive that creates large numbers of orphaned orangutans. If economic considerations are used as a basis for normative decision making, killing mother orangutans and selling their infants

Figure 2.9. Actions associated with the problems of and potential solutions for orphaned orangutans (*Pongo pygmaeus*) in Indonesia, the motives that drive them, and the legal and ethical restraints that constrain such motives and their effects.

in pet markets makes sense. Even with the risk of arrest and fines or imprisonment, the financial reward is great enough that the cost–benefit ratio leans heavily in favor of continuing these practices. Such practices are restrained, if imperfectly, by conservation laws that are intended to support a view of the intrinsic value of the orangutans and of overall biodiversity, but economic profit, manifested as bribery and corruption within the ranks of the enforcement officers and government officials, often overwhelms social and legal affirmations of the orangutan's intrinsic value. Nevertheless, some individuals, perceiving the worth of the species "on its own," respond with compassion toward the needs of orphaned orangutans. Scientists valuing world biodiversity and the opportunity to study and learn about orangutans inform the rehabilitation effort through careful studies of orangutan diets, social and reproductive behavior, and habitat needs. But the actions prompted by these motives are themselves constrained by a lack of financial and human resources. The government of Indonesia does not value orangutans enough to divert scarce resources from pressing human needs to build more rehabilitation centers or hire more workers to rehabilitate apes. And people in other nations do not provide enough money to OC and other conservation organizations to finance a complete solution. Ironically, just as economic motives helped to create the problem, economic restraints perpetuate it. Many conservationists believe that even after release in a "protected" area in Indonesia, economic motives for profit from such reserves, especially timber and mining, will undermine laws established to protect the reserves and the orangutan, as well as other elements of Indonesia's natural heritage.

Not every species is as charismatic, intelligent, or physically similar to human beings as an orangutan. But regardless of what species conservation efforts try to protect, every conservation biologist must realize that conservation values and virtues, at personal and legal levels, are essential for the effort to succeed. Until local residents and the international business and trade community incorporate a conservation ethic that sees intrinsic value in the orangutan, it will continue to make sense to capture young orangutans and sell them as pets to realize their instrumental value as economic profit. Until more affluent people in Indonesia and around the world see the importance of practicing conservation virtues like those described earlier by Bouma-Prediger (1998), especially virtues like frugality and self-restraint that curb demand for tropical forest products and their associated habitat destruction, the endangerment of the orangutan will remain a significant conservation problem.

2.6. Synthesis

Values are the engine of action. Although economic valuations can, theoretically, attribute some measure of worth to all types of values, economic assessments often mistakenly assume that value should be based on human preference, need, or desire, rather than on moral obligation, ideal outcome, or the intrinsic worth of the object. Aldo Leopold wrote, "The 'key-log' which must be moved to release the evolutionary process for an ethic is simply this: quit thinking about decent land use as solely an economic problem. Examine each question in terms of what is ethically and esthetically right, as well as what is economically expedient" (Leopold 1966:262).

By affirming normative postulates of what constitutes "decent" and "right" in conservation and not merely what is "economically expedient," conservation biology inherently aligns itself with the philosophical position that biotic resources have intrinsic worth. Therefore, one of the fundamental problems of conservation biology is to determine the basis of intrinsic worth, make meaningful assessments of intrinsic value, and then promote policies and behaviors that reinforce such value.

Values in conservation are not fact-independent sentiments supported merely by assertion, nor are they to be used as tools to manipulate people of different convictions into doing what conservationists want. Values are subject to inspection and analysis, and must be rooted in sound philosophical and intellectual frameworks to be persuasive. In a global community, it is essential that conservation biologists appreciate the intellectual content and ethical context of expressions of values and their motivations in different individuals and cultures. Conservation biologists must treat these systems with intellectual integrity and respect, and continue to learn from such systems in ways that allow them to better understand, articulate, and practice their own values as conservation biologists. In the same way, conservation biologists must be prepared to change their own behavior as they become informed by traditions of values and ethics from different sources, and even be prepared to make intellectual commitments to particular systems of value. Commitment to an ethical system of values does not lead merely to greater self-understanding and ability to persuade others to take right action, but to becoming a person who has a firm disposition and character to always act for the best and highest good in conservation, an individual possessing a high degree of conservation virtue.

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3

The Legal Foundations of Conservation Biology

By the law of nature, these things are common to mankind – the air, running water, the sea, and consequently the shores of the sea

Emperor Justinian 533 BC, translated by T. C. Sandars 1997

In this chapter, you will learn about:

1. **The development and contemporary expressions of conservation law and its relationship to the science of conservation biology**
2. **The most important international conservation laws and how they define and empower conservation**
3. **Examples of national conservation laws in the United States that have provided models for conservation at national levels in other countries**
4. **Specific case histories in which national and international conservation laws have influenced the goals and practices of conservation biology**

3.1. Conservation Law and Policy

3.1.1. Context and Definition

Conservation biology is a legally empowered discipline; that is, it represents a scientific community that has received legal, political, and cultural incentives and reinforcements. Indeed, some have gone so far as to call conservation biology a "regulatory science" that "seeks to develop scientific standards that can be applied to regulatory criteria and then to develop management strategies to meet those standards" (Tarlock 1994:1130). Throughout the world, the goals of conservation biology, including preservation of biodiversity, protection of endangered species, and conservation and management of ecosystems, are increasingly established in and enabled by laws.

Today many conservation biologists are tempted to believe that it was conservation biologists who inspired the laws that protect biological diversity, but a close look at recent history forces us to abandon this self-gratifying notion. It was conservation law that came first, in manifestations like the US Endangered Species Act (1973) and the Convention on the International Trade in Endangered Species (1973), among others that preceded the earliest organizational efforts to define the discipline of conservation biology. Although conservation biology might still have developed without national and international environmental legislation, it would have been substantially less influential. In fact, conservation biology owes much of its early success and continuing vitality to its legal empowerment and support, and modern national and global environmental legislation has affected and continues to affect conservation biology in three ways. First, it has given legal incentives and approval for biodiversity preservation. Second, it has affirmed the goals of conservation biology and influenced the public to value conservation. Third, it has provided an environment that requires and sustains scientific research, management and monitoring.

Good science and its attendant empirical data are necessary, but insufficient, for achieving conservation biology's goals of stemming species extinction and ecosystem degradation (Meffe and Viederman 1995). Conservation biology, as a discipline, asserts that scientists can and should influence environmental policy. To do this, they must first comprehend both science and policy. Despite the advantages of legal empowerment, conservation biology's ties to law and policy are not always beneficial. On one hand, laws represent current social values. But laws also shape values for future generations, codifying aspirations or preferences into something more lasting and transcendent. Laws empower action, providing political resources and social force to achieve specific goals, but laws also limit action by setting arbitrary and fixed boundaries that may not correspond to the needs of dynamic systems. Because laws are difficult to repeal, they provide a sense of permanence to the values they establish. But laws also can become rigid, unresponsive to changing conditions, and ultimately ineffective in solving the problems they were enacted to address.

Traditionally, scientists have avoided involvement in law- and policy-formulation because they believed that such involvement would undermine their professional objectivity and public credibility; however, many conservation biologists disagree. Reed Noss, a former editor of the discipline's most well known journal – *Conservation Biology* – said, "I believe that conservation biologists have a responsibility to enter the policy arena and advocate both general principles and specific actions needed to conserve biodiversity" (Noss 1993). Putting the matter more forcefully, conservationists Dwight Barry and Max Oelschlaeger stated, "Advocacy for the preservation of biodiversity is part of the scientific practice of conservation biology" (Barry and Oelschlaeger 1996:905). But "advocacy," if it is to be effective advocacy, must ultimately be advocacy for laws and polices that protect biodiversity. For this reason, the issue of conservation advocacy and the relationship of conservation advocacy to conservation policy remain at the forefront of concern and debate among conservation biologists (Brussard and Tull 2007). Connections to conservation law and policy are intrinsic to conservation biology's continuing mission, as well as essential to understanding its historical development.

Policy is distinct from law as being the necessary outcome of all laws that are actually enforced, and can be defined as "a definite course or method of action selected from among alternatives and in light of given conditions to guide and determine present and future decisions" (Merriam-Webster 2003). More specific to our context, environmental legal scholars James Salzman and Barton Thompson define *environmental law and policy* as "the use of government authority to protect the natural environment and human health from the impacts of pollution and development" (Salzman and Thompson 2003:1).

Legal scholars acknowledge two general views of international law, including international conservation laws. The first of these, known as the ***positivist view***, holds that international law consists of neutral rules. In this view, the goal of national governments and international agencies is to enforce rules. A second view, known as the ***process view*** holds that international law provides the normative framework and procedures for coordinating behavior, controlling conflict, facilitating cooperation and achieving values (Weiss 1999:100). In the realm of international conservation law, it is this process view that seems to best describe actual behavior, particularly in democratic nations. The process view is the paradigm that we will follow in this chapter to understand conservation law and its effects at both international and national levels. This is because, in democracies, laws originate with issues that gain the attention of politicians and government bureaucrats. But issues do not become law and laws are not translated into policies without lengthy examination and development by all concerned parties because one of the main functions of law is to provide a framework for legitimating social norms. Laws are specifically aimed to influence behavior and reinforce approved values by establishing normative rules that everyone must follow or face punishment. Environmental and conservation law often drive ongoing conservation efforts and environmental protection, but, to be effective, law must eventually be supplemented by attendant policies that support and clarify its intentions. For our purposes, we will define "policy" as *a set of principles and intentions used to guide decision making*. We may define "environmental policy," in which conservation concerns are embedded, as *a set of principles and intentions used to guide decision making about human management of natural capital and environmental services* (Roberts 2004:1–2). It is impossible to separate conservation law from conservation policy, and fruitless to try. We will begin with an examination of how conservation law began to develop, and then examine the international and national policies for species and habitat protection that sprang from it.

3.1.2. Historical Origins of Conservation Law

Environmental and conservation law are rooted in three conceptual frameworks: ethical rights, utilitarian interests, and equitable distribution of risks (Salzman and Thompson 2003:26). As noted in Chapter 1, the earliest laws addressing the use or treatment of plants and animals were rooted in concepts of ethical rights. In ancient Roman, Chinese and Jewish legal traditions, animals and, in some cases, even the land itself, were protected from certain forms of abuse and mistreatment. Although the intention of such laws, particularly toward animals, was not directed toward "conservation" as we understand it today, but rather towards dispensing justice, these traditions did establish a basis for treating non-human creatures and ecosystems as *moral subjects*. That is, non-human entities in the natural world were perceived as "morally considerable," they could be treated in a morally right or wrong manner.

A second category of laws, also noted in Chapter 1, were prohibitions against the use of plants or animals found on private property, especially if the private property belonged to nobility. In some ways, these laws also were concerned with rights, but, in this case what was protected was the right of the landowner to enjoy a healthy, productive, or aesthetically beautiful environment. Although such laws achieved a measure of protection for non-human species, the rights they protected were expressions of privilege, not expressions of conservation. Laws of this type were rooted in utilitarian interests of the landowner. It is worth noting now, because you will see examples of it later, that conservation laws arising from concepts of rights, grounded in moral values, tend to advocate complete protection for the entity to be conserved, regardless of costs. In contrast, laws rooted in utilitarian interests use cost-benefit analyses (Chapter 2) as the primary guide to making the correct or "right" decision. In such a view, costs are not irrelevant, but rather the most relevant and decisive decision-making factor.

Historically, there were notable and commendable exceptions to the pattern of making conservation serve only as an expression of privilege for the fortunate few. Asoka, an Emperor of India, proclaimed and enforced an edict for the protection of mammals, birds, fish, and forests in 252 BC. In The Netherlands, King William of Orange set aside the Wood of the Hague in 1576, not for his own personal pleasure, but for the protection of the place itself. In 1669, the French statesman Jean Baptiste Colbert, with the full permission and support of the king, issued an ordinance to protect French forests from overcutting. In this case, Colbert's motives may have been influenced by his aims to establish a French navy and mercantile fleet that would provide increased trade, wealth, and protection to his nation, but it protected French forests nonetheless.

3.2. Environmental and Conservation Law in Individual Nations: Modern Examples from the United States, South Africa, and Australia

3.2.1. General Considerations

Although Colbert's actions influenced international relations and trade, they were taken in the interests of a single nation. While international cooperation through international conservation law is critical to the world conservation enterprise, much of international conservation law has been crafted from laws that were first developed in individual nations. Even today, with a strong and growing body of international conservation law designed to empower the world conservation effort, international laws and treaties invariably suffer constraints that cannot be overcome at international levels. By the very nature of the diversity of nation states, international conservation agreements often descend to a 'least common denominator' approach in species and habitat protection, usually united around trade or other forms of economic interests. The actions really needed to preserve endangered species and their habitats must almost always be resolved at national and local levels, not only because that is where local breeding populations are resident, but because only in national and local communities can one hope to achieve a consensus of shared values that can support more aggressive and effective actions needed to achieve real conservation goals. Further, even international conservation laws become meaningless without national and local enforcement. The participation of ordinary citizens in conservation requires engagement at these levels, and such participation is essential for both enforcement and monitoring.

For these reasons, we now take up examples of national conservation legislation from three countries, the United States, the Republic of South Africa, and Australia. These examples will illustrate how conservation law is formed at national levels, how public participation is facilitated to strengthen enforcement and develop workable policies, how conservation laws can actually achieve conservation goals, and how problems that limit the effectiveness of conservation law can be identified and overcome. We will begin with the US National Environmental Policy Act (NEPA) and the US Endangered Species Act (ESA), two laws that have been so effective that they have been exported and "cloned" repeatedly throughout the world. Their influence is no longer national, but global, and understanding them adds value to conservation in every context throughout the world. From this foundation, we will examine more recent developments of national conservation laws in the Republic of South Africa and Australia that incorporate radical new conservation concepts, concepts that are increasingly being examined and debated in the global conservation community. But, for our first two examples, we must provide some context to understand, more generally, how conservation law became a significant issue in the US, as a means of understanding its development in democratic societies.

Beginning with the signing of the National Environmental Policy Act on January 1, 1970, that decade witnessed the development of a number of innovative structural and legal arrangements in conservation laws in the United States. Three arrangements developed during this decade that were designed to promote greater public participation. These were; (1) liberal provisions for public participation; (2) expanded rights for private organizations and individuals to sue public agencies; and (3) provisions for intervenor funding for legal expenses. Legal challenges to federal agencies' environmental actions began in 1971 and ultimately led the US Supreme Court to affirm the right of private citizens and non-governmental organizations to sue agencies for harmful or potentially harmful environmental actions. Other court decisions established the ability of citizens and NGOs to halt proposed actions by federal agencies if the environmental impact statements were judged to be improperly prepared. NEPA's requirement for environmental impact statements (EIS) accompanying proposed actions by federal agencies along with the success of citizen-led litigation demonstrated the power of the legal process and public input in achieving conservation goals.

3.2.2. Common Characteristics of Effective National Conservation Law

Although laws addressing conservation issues are diverse, the most powerful and effective among them share important characteristics that are now common in conservation laws of individual nations throughout the world. Their shared traits include an inspirational and radical message, the potential for growth in influence, an ability to attract and hold the interest of scientists because they raised questions that must be answered by research, and a requirement for monitoring (Rodgers 1994).

The inspirational and radical message of the strongest modern environmental and conservation laws built a strong foundation of moral and social support. Although court interpretation often has been necessary for the message to be clarified and implemented, such a message has been latent within all truly effective conservation legislation. Legal scholar and law professor William H. Rodgers Jr., speaking of common characteristics of exemplary US environmental laws, said of these that "they lack the compromised and ambiguous form normally associated with an act of Congress" (Rodgers 1994). Indeed, the most effective statutes in US environmental law were almost brazen in their language, and inspired popular support. The potential for growth in influence allowed such laws to alter social values, and they gained and held scientific support because they defined tasks for scientists to perform and questions for them to answer.

Several themes of US environmental legislation have become part of conservation biology, and are especially prominent in NEPA and the ESA. Such legislation has (1) required that pollution or environmental degradation be evaluated in the context of ecosystem function (NEPA); (2) endorsed intrinsic and non-economic values for resources and non-human creatures (ESA, NEPA); (3) emphasized the status of individual species and affirmed that extinction is undesirable (ESA); (4) stated that renewable resources were to be managed sustainably, and that managers of non-renewable resources must take into account the permanent consequences of present management actions (NEPA); (5) made federal funding available for research and habitat acquisition (ESA); (6) provided citizens and NGOs with avenues for participation in decision-making and litigation against federal agencies (ESA, NEPA); and (8) given additional power to agencies to protect resources (ESA, NEPA).

Environmental and conservation laws have provided conservationists with the legal means to stop activities harmful to the environment or to particular species, especially on federal lands or on projects receiving federal funding or requiring federal permits. Of these, the National Environmental Policy Act and the Endangered Species Act, passed and enforced separately but often interacting legally, have radically altered the practice and enforcement of conservation values in the United States and, by imitation, throughout the world. More than any other legislation, the radical transformation of conservation law achieved by these two acts created the legal environment and social values in which conservation biology operates today.

3.2.3. The US National Environmental Policy Act (NEPA)

3.2.3.1. NEPA's History and Content

In 1966 a professor of public administration, Lynton K. Caldwell, published a paper entitled "Administrative Possibilities for Environmental Control" (Caldwell 1966). In his paper, Caldwell suggested that qualitative environmental standards could provide the administrative coherence historically lacking in natural resource policy (Caldwell 1966; Tarlock 1994). Caldwell's paper, published in the book *Future Environments of North America* (Darling and Milton 1966), would become one of the most influential publications on environmental policy of the late 1960s.

The US Congress employed Caldwell as the principal drafter of a law that was designed to be the centerpiece of a new era of environmental and conservation legislation, the National Environmental Policy Act of 1969 (Tarlock 1994). In writing NEPA, Caldwell mandated that a "detailed statement" must accompany "proposals for legislation and *other major federal actions significantly affecting the quality of the human environment*" (emphasis added). This requirement led to the development of the now-familiar environmental impact statement (EIS) that describes the possible environmental effects of actions proposed by federal agencies. Ultimately, policies and procedures associated with preparation of an EIS led to pervasive and well-defined procedures for public involvement, as well as for challenging an EIS in court.

NEPA was signed into law by President Richard Nixon on January 1, 1970, a fitting beginning to what would be called "the decade of the environment." NEPA stated a national policy for the environment and formally established environmental quality as a leading national priority. NEPA expressed its "inspirational and radical message" in these words: "It is the continuing responsibility of the federal government to use all practicable means, consistent with other essential considerations of national policy, to improve and coordinate federal plans, functions, programs, and resources to the end that the nation may: (a) fulfill the responsibilities of each generation as trustee of the environment for future generations, (b) assure for all Americans safe, healthful, productive, and esthetically and culturally pleasing surroundings, (c) attain the widest range of beneficial uses of the environment without degradation, … (d) preserve important historic, cultural, and natural aspects of our natural heritage, … (e) achieve a balance between population and resource use which will permit high standards of living and a wide sharing of the amenities of life, and (f) enhance the quality of renewable resources and approach the maximum attainable recycling of depletable resources." Robed in such positive platitudes, NEPA passed both houses of Congress with relatively little opposition.

In fact, it was not NEPA's high-sounding rhetoric in its opening section that would have significant impact on US environmental policy. Hidden in the more mundane language of the bill were words that would profoundly affect the practices and decisions of every US federal agency. The requirement that all federal agencies develop information, in the form of a "detailed statement," on the ecological consequences of their actions and weigh these impacts in their decision- and policy-making would become the "teeth" of NEPA's enforcement power. Each such "detailed statement" must describe (1) the environmental impact of the proposed action, (2) any adverse environmental effects that cannot be avoided should the proposed action be implemented, (3) alternatives to the proposed action, (4) the relationship between local, short-term uses of the environment and the maintenance and enhancement of long-term productivity, and (5) irreversible or irretrievable commitments of resources involved in the proposed action should it be implemented. Such a statement is then circulated among government agencies and public venues (NGOs, libraries, and private citizens groups) for comment.

NEPA was unique among environmental and conservation legislation in several ways. First, it was proactive rather than reactive, forcing government agencies to consider the environmental effects of proposed actions in advance. Second, NEPA forced government agencies to explicitly consider the value of non-economic resources, ensuring that conservation would be considered in evaluating the proposed action. Finally, NEPA introduced environmental assessment as a means to guide administrative decision-making (Caldwell 1966; Tarlock 1994). Thus, NEPA not only established a mechanism for environmental review, but also stimulated an increased level of citizen involvement in environmental decision-making. Policy analyst Richard A. Liroff summarized the true significance of the act when he noted, "Implicit in NEPA was the notion that the public was to be informed of the rationale underlying environmentally impacting administrative actions. NEPA's architects also sought public involvement in decision making, but they did not indicate when it should occur or what form it should take" (Liroff 1976:88). It is also noteworthy that NEPA was strongly linked to the kind of "ideal" role of government in conservation that had first been developed by Theodore Roosevelt (Chapter 1), embodying his ideal of environmental protection resting on a foundation of scientifically-informed government decisions modified by citizen input.

These implicit notions of public participation ultimately became explicit directives for public involvement, first addressed by the courts in the case of *Calvert Cliffs v. the Atomic Energy Commission* of 1971. In this case, the US District of Columbia Court of Appeals ruled that federal agencies must comply with the procedural requirements of NEPA, including compliance with the preparation of a detailed statement describing the environmental impact of a proposed action, and that this requirement was in force even for an action by a private company or private individuals on private land if the action required a permit from a federal agency. *Calvert Cliffs* added legal precedent and enforcement toward motivating US federal agencies to take seriously the requirement for an EIS for proposed actions on federal land or "major federal action" that required federal permission. To better understand the scope of NEPA's effect, one must understand what constitutes a "major federal action" and appreciate the extent of federal lands in the United States and their general management directives.

3.2.3.2. NEPA and US Federal Lands

The US government is the nation's largest landowner, with responsibility for more than 715 million acres, one-third of the total US land area. Many of the country's western states are largely public domain; more than half of the land in Alaska, Nevada, Idaho, Oregon, Utah, and Wyoming is federally owned (Rosenbaum 1985). On or underneath this land area lies a wealth of natural resources. Perhaps one-third of all remaining US oil and gas reserves, 40% of coal reserves, 80% of shale oil reserves, more than 60% of low-sulfur coal (Rosenbaum 1985), and sites with high potential for geothermal energy generation exist on US public lands.

A "federal action" takes place on federal lands using federal funds, or on private, state, or locally owned land, if the action requires a permit from a federal agency. Any of these situations constitute the "federal hook" that activates the NEPA process. The agency involved may fulfill NEPA's requirements of a "detailed statement" by preparing an environmental assessment (EA) that results in a "finding of no significant impact" (FONSI) or requires additional review with an EIS. Federal actions like routine maintenance, management, and structural repairs are "Categorically Excluded" (CatEx) from further review and do not require the development of an EA. Most federal projects are classed as CatEx or their review is completed with an EA/FONSI.

If an EA is required, the process could be described as a kind of "mini-EIS." An EA may be prepared by an agency as part of a preliminary analysis to determine if a full-scale EIS is required. An EA must contain (1) a clear and concise description of the proposed action; (2) a detailed description of the environment affected by the proposed action; (3) an assessment of the probable effects of the proposed action; (4) an evaluation of the probable cumulative and long-term environmental effects, both positive and negative; (5) an assessment of the risk of credible potential accidents; (6) a description of the relationship of the proposed action to any applicable federal, state, regional, or local land use plans and policies; and (7) a brief description of reasonable alternatives and their probable environmental effects, one of which is required to be that of not implementing the proposed action, the so-called "no action" alternative.

An EA differs from an EIS in scope, length, and detail; however, an EA also includes procedures for public input and requires substantial agency investments of time, effort, and money. If the agency determines that an EIS is not required, it will then publish a finding of no significant impact, which is a brief document that explains why the proposed action has no significant effect on the environment. The FONSI must describe the action, the alternatives considered, and the environmental effects and the reasons why they are not significant. Individuals or groups unsatisfied with the FONSI, or with the EA in general, can take the agency to court for not preparing a full-scale EIS.

3.2.3.3. Preparation of an Environmental Impact Statement

The NEPA process typically begins when an agency publishes a notice of intent (NOI). The NOI identifies the responsible agency (if an action involves two or more agencies, one is designated the "lead agency" and assumes responsibility for the EIS) and describes the proposed action. Invitations, procedures, dates, times, and locations of public meetings, with availability of related documents, also are listed. Minimally, the NOI will be published in the Federal Register and mailed to individuals who request it, individuals known to be interested in the proposed action, and national organizations expected to be interested in it. The NOI may also be in local newspapers, publicized through local media, and posted on the site to be affected (Murthy 1988).

As a first step in preparing the EIS, the lead agency will assemble an interdisciplinary team of professionals capable of assessing the scientific, social, and economic issues likely to be addressed in the EIS. A team leader coordinates the group's activities to produce the EIS within specified guidelines and deadlines, and assembles comments from other team members, other agencies, experts, and the public.

EIS preparation requires regular contact among the lead agency, other cooperating agencies, and the public. Public-issue identification or "scoping" meetings involve the public early in the process. Scoping is "an early and open process for determining the scope of issues to be addressed and identifying the significant issues related to a proposed action" (Yost and Rubin 1989). After it is completed, the lead agency prepares an EIS implementation plan (IP) and uses it to produce a draft EIS (DEIS).

The lead agency conducts an internal review of its DEIS and then publishes a "notice of availability" (NOA) in the federal register. Public comment on the DEIS, including comments received at public meetings where the DEIS is presented and explained, is then received, considered, and, if appropriate, incorporated into a revision of the EIS. From this effort, a review draft of a final EIS (FEIS) is prepared, reviewed within the agency, and made available to the public. Considering information presented in the final EIS, the responsible official of the lead agency decides whether to implement the proposed action or one of the alternatives (including the possibility of the "no action" alternative) and publishes the decision in the federal register. This "record of decision" (ROD) like other NEPA-associated documents, is available to the public and other agencies. Anyone who disagrees with the decision has 30 days to file an appeal. If an appeal is granted, the decision may be overturned and the EIS might have to be rewritten.

Policy analyst Richard A. Liroff has provided a key to understanding NEPA's profound effect on national environmental policy by noting that "… NEPA laid the groundwork for a series of procedures whereby environmental considerations could be fed into agency decision-making routines" (Liroff 1976:210). These procedures for environmental assessment radically changed the pattern and process of agency decision making with respect to public lands. Most US states now have their own versions of NEPA. In addition, procedures for public input established by agencies and by US courts in response to NEPA set the example for public input requirements in most subsequent environmental and conservation legislation. More than any other statute, NEPA made environmental review a permanent part of environmental decision making in the US. This change profoundly affected the development of conservation biology because it made conservation issues relevant and legally mandated considerations in all proposed actions on public lands. In addition, NEPA transformed US environmental and conservation policies into arenas for public participation rather than simply expressions of elected representatives. Informed by such participation, the public in general, and scientists as public citizens, began to see clearer connections between conservation science and conservation law, and to use these connections as conservation advocates.

POINTS OF ENGAGEMENT – QUESTION 1

How does the Environmental Impact Statement (EIS) make NEPA a proactive rather than reactive conservation law? How does the EIS shift the "burden of proof" between developers and conservationists?

3.2.3.4. Shortcomings of the National Environmental Policy Act

It has been over 3 decades since NEPA and its grand design for a national environmental policy became law in the United States. Although NEPA has grown in influence, not all of that influence has been positive. With its successes, NEPA also has had negative consequences that its planners did not anticipate.

One of the most foundational tensions in NEPA was that it assumed an ecosystem management approach before there were well-developed concepts and procedures of ecosystem management (Chapter 12). Specifically, NEPA's intent is to provide for functioning, sustainable ecosystems and long-term environmental quality. However, its highest level mechanism, the Environmental Impact Statement, is usually prepared by one administrative unit of a single federal agency, such as the staff of a national forest within the US Forest Service, operating within fixed spatial boundaries, limited jurisdiction, and strong vested interests in particular commodities. NEPA procedures demand that the lead agency identify and inform stakeholders, but its procedures do not truly involve stakeholders as full partners in the decision-making process. The public can express concerns at scoping meetings, through letters, or by direct contact with agency personnel, but the actual preparation of the EIS is solely the responsibility of the agency's interdisciplinary team. Although the public can give additional input after reviewing the draft EIS, such input is strictly one-way communication. The public speaks, the agency listens, but the final EIS remains an internal agency product. As a result, if the public is still dissatisfied with the outcome of the final EIS and the Record of Decision that accompany it, they have little choice but to litigate. The purpose of such litigation is, regrettably, not to improve the EIS or its decision but to show that the EIS is inadequate on professional and scientific merits as a basis for the management decision, and therefore must be thrown out and done over. This approach necessarily forces the agency into the position of defending its own EIS, if only to save the taxpayers money and their personnel more work, and an adversarial climate is created between the agency and the public. Thus, NEPA often has multiplied litigation rather than improved decision making. Faced with the daunting prospect of intense adversarial litigation, resource management agencies have responded by diverting more agency resources and personnel solely to the production of environmental impact statements to make their EIS's "litigation proof." The price for such administrative prudence is high. Money is diverted from field research and management to salaries for specialists in EIS preparation, fees for consultants who collect data solely for documentation in the EIS, and legal expenses for ongoing litigation of EISs under appeal. Agency administrators and scientists spend less time in the field and more time preparing or defending NEPA documents. Trust between agencies and public diminishes rather than increases. Some policy analysts have argued for new, more creative approaches in the NEPA process. These have included such novel propositions as the "citizen jury," in which members of the public evaluate the EIS and determine the decision by consensus, rather than the agency (Brown and Peterson 1993), or the use of informal advisory groups that would have continuing input to the agency's interdisciplinary team (Sample 1993). However, neither these nor other, even more novel concepts for solving the problems of NEPA have been tested in real cases (Goetz 1997).

Some experts now argue that NEPA will become more effective, and its true intent more manifest, as US resource management agencies mature in their understanding of and commitment to ecosystem management approaches. There is some evidence in individual agencies that, in fact, this is the case, with more recent EISs and decisions, particularly in the Forest Service, reflecting more fully the true intent of NEPA in ecosystem protection and less of simply following the rules of an administrative procedure (Goetz 1997). NEPA and the EIS have unquestionably shaped the landscape of US policy and administration in ways that profoundly affect the perception and practice of conservation biology. But whether NEPA will ripen to bear the fruit of its full intent depends largely on whether agency and public interests mature into working relationships for conservation or remain conflicts of litigation and mistrust between adversaries.

3.2.4. The US Endangered Species Act

3.2.4.1. Historical Origins and Content

The Endangered Species Act (ESA) has been called the "strongest and most comprehensive species conservation strategy" in the world (Rohlf 1995). The ESA affirms the value of biodiversity, and actions authorized under the ESA have contributed to the persistence of many endangered species, and even the complete recovery of a few, such as the bald eagle. As of July 2007, 1,352 native species (746 plants and 606 animals) had been listed (US Fish and Wildlife Service 2007), The endangered species act might be the world's most admired piece of conservation legislation, but it is also one of the most controversial. No other conservation statute has so influenced the development of conservation biology or engendered so much enduring hostility and withering criticism.

First passed in 1966 as the Endangered Species Preservation Act, the original law was adopted with little controversy or fanfare, and little power. It limited protection to vertebrates native to the US, provided authority for only modest land acquisition for habitat, focused on populations in existing wildlife refuges, created no new programs or legal power and was so vague as to be meaningless. Its immediate successor, the Endangered Species Conservation Act of 1969, was not much better, although it broadened the definition of "fish and wildlife" to include invertebrates and prohibited the importation of endangered foreign species except for scientific purposes (Nash 1989; Smith 1992). These legally-toothless statues were rewritten in 1972 by E. U. Curtis Bohlen, then Undersecretary of the US Department of Interior, in ways that profoundly changed the legal landscape of conservation in the United States. Bohlen's contribution was essentially a new law rather than simply a revision of the former statutes. The new version expanded the jurisdiction of the ESA from vertebrates to most plant and animal species. The 1973 ESA legally defined a "species" as "any subspecies of fish or wildlife or plants, and any distinct population segment of any species or vertebrate fish or wildlife which interbreeds when mature." Although this definition is not scientifically or intellectually satisfying (it assumes an understanding of the very concept it is attempting to define), it is comprehensive in specifying an enormous array of organisms eligible for protection. Bohlen's rewritten ESA also created a new category for legal protection called "threatened species," and even allowed the listing of species that were threatened only in a portion of their range. The 1973 ESA also introduced the concept of "designated critical habitat" into environmental law, creating the legal provisions that require not only the protection of the species, but also the land or water in which it lives. The 1973 ESA gave primary authority for enforcement of the ESA to the Department of Interior's US Fish and Wildlife Service (FWS) for cases involving terrestrial and freshwater species and to the National Marine Fisheries Service of the Department of Commerce for marine species. FWS also has authority to identify and purchase such critical habitat, and to stop activities on such habitat that threatened the species, even if the habitat was privately owned. The ESA also offers incentive for the federal government to initiate cooperation with state programs as well as to cooperate fully with existing state programs to protect species (Section 6). For example, the Act states explicitly that the Secretary of the Interior shall "cooperate to the maximum extent practical with the States," may enter into management agreements "with any State for the administration and management of any area established for the conservation of endangered species or threatened species," and that the Secretary is authorized to "enter into a cooperative agreement … with any State which establishes and maintains an adequate and active program for the conservation of endangered species and threatened species." In fact, the ESA actually helped to stimulate the kind of federal-state cooperation it envisioned by its very existence because, after its passage, many states passed state endangered species laws modeled on the ESA.

It was Bohlen's skill and political savvy in rewriting the Endangered Species Act that changed a formerly obscure statute into what Donald Barry, a former vice president of the World Wildlife Fund, called "the pit bull of environmental laws.... It is short, compact, and has a hell of a set of teeth. Because of its teeth, the act can force people to make the kind of tough political decisions they wouldn't normally make" (quoted in Rosenbaum 1995:334). The 1973 Endangered Species Act passed both houses of Congress with near-unanimous support.

The ESA gives the FWS responsibility for identifying endangered species and proposing these species for protection through the "listing" process (Figure 3.1). However, actual listing is normally accomplished through interagency consultation, as specified in the ESA's Section 7, because the ESA authorizes *all* federal agencies to "utilize their authorities in furtherance of the purposes of this Act by carrying out programs for the conservation of endangered species and threatened species …". The ESA, like NEPA, also provides for review of actions carried out by agencies to ensure that their actions do not "jeopardize the continued existence of any endangered species or threatened species or result in the destruction or adverse modification of the habitat of such species …".

In assessing such actions the Act defines an "endangered" species as one that is "in danger of extinction throughout all or a significant portion of its range." A "threatened" species "is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." In managing an endangered or threatened species, the FWS also must define ***critical habitat*** – (habitat of special significance to the species' survival; Bean et al. 1991) and develop a recovery plan that will restore the species to secure population levels. The ESA also provided explicitly for public participation in the listing process. Any citizen or private citizen's group may petition the Secretary of the Interior to add a species to the endangered species, list, and the Secretary must respond with a determination for or against the petition (in the words of the Act, "warranted" or "unwarranted") within 90 days after it has been filed. Given its broad powers and uncompromising standards, the ESA was in many ways too comprehensive and too rigid to go unchallenged indefinitely. The most famous such challenge began in 1978. In *Tennessee Valley Authority v. Hill*, the Supreme Court ruled that the Tellico Dam on the Little Tennessee River could not be completed because the dam would destroy the habitat of an endangered fish, the snail darter (*Percina tanasi*) (Figure 3.2). Although environmentalists won the battle in court, their victory cost them the war in congressional backlash at what many representatives now perceived as an act that was too restrictive and insensitive to human need. Within a year, Congress had amended the ESA to create a committee that could waive the law's regulations under special economic conditions. Although officially called the Endangered Species Committee, this group soon became known as the "God Squad" because of its power to revoke the ESA's protection for selected species. The Committee ruled in favor of the fish, but Congress responded by excluding the snail darter from protection under the ESA. As for the obscure species that caused all the trouble, snail darter populations were transplanted and established in other streams, and the Tellico Dam was completed.

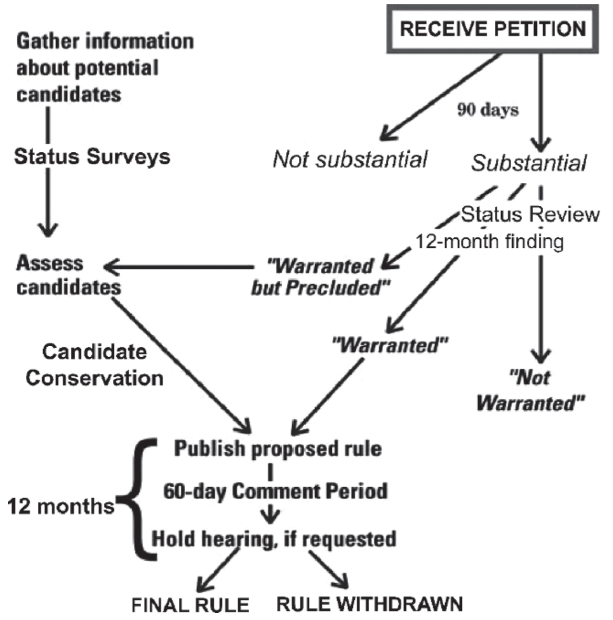

FIGURE 3.1. The process through which a species becomes "listed" as Endangered under the provisions of the US Endangered Species Act. (Diagram courtesy of US Fish and Wildlife Service.)

FIGURE 3.2. The snail darter (*Percina tanasi*), a fish that delayed the construction of the multimillion dollar Tellico Dam on the upper Tennessee River, USA, by virtue of its protection under the US Endangered Species Act. (Photo courtesy of US Fish and Wildlife Service.)

The FWS is prohibited from considering economic effects in decisions regarding the listing of a species, but amendments to the ESA added the requirement that the FWS conduct an economic analysis of the effects of designating critical habitat. Because such designation usually involves the suspension of other activities in the area, including economically profitable ones, the amended ESA includes an "exclusion process" through which all or part of the critical habitat may be excluded from protection if the economic analysis determines that the cost of protection poses too great a hardship in economic or other forms of loss. As in NEPA, a public comment period is provided to allow interested parties to provide information that can be included in the analysis (Berrens et al. 1998).

Post-1973 amendments made the ESA more flexible in resolving conflicts, but also, in the eyes of many conservationists, weakened and betrayed the Act's original intent to preserve endangered species regardless of economic cost (Nash 1989). Nevertheless the ESA remains armed with formidable provisions to protect listed species and is a cornerstone of biological conservation.

The process of designating critical habitat is the most frequent source of conflict between the federal government's interest in protecting endangered species and the interests of private landowners. Although the ESA provides for "informed consultation" between the federal government and landowners to determine a mutually satisfactory plan to protect the species without undue infringement of personal property rights (Section 7), private landowners have not always been satisfied with the outcome. In fact, many private landowners assert that the ESA prohibits them from deciding how to use their own land and violates fundamental rights associated with private property. Critics claim that the ESA's punitive approach to dealing with landowners who violate the Act's provisions when endangered or threatened species are found on their land is its biggest weakness because the threat of punishment often promotes landowner behavior that is harmful to the protected species. As Myron Ebell, a property-rights advocate, has said, "… if there is an endangered species on your land, the last thing in the world you want to do is provide habitat for it" (Cooper 1999). To reduce landowner-government conflicts, one recent strategy employed by the federal government is the ***habitat conservation plan*** (HCP). To better understand the need for and development of HCPs, we look to the problems associated with the protection of a particular species, the red-cockaded woodpecker (*Picoides borealis*).

3.2.4.2. The Endangered Species Act and Landowner Conflicts: The Case of the Red-Cockaded Woodpecker

The red-cockaded woodpecker (Figure 3.3) inhabits the southeastern United States where it usually lives in stands of mature longleaf pine woodlands. The woodpecker prefers open forests with minimal understory, a condition that can be maintained only by recurrent fires and active understory management. During the mid-1900s, the red-cockaded woodpecker had declined in abundance to fragmented populations of only a few to several hundred individuals, with a total population of less than 15,000 birds.

FIGURE 3.3. The red-cockaded woodpecker (*Picoides borealis*), an endangered species that has been the subject of intense management through habitat conservation plans. (Photo courtesy of US Fish and Wildlife Service.)

Most of the historical habitat for the woodpecker is on privately owned land. Landowners typically fear the federal regulations that would be imposed on their land and their use of it if red-cockaded woodpeckers were discovered on their property. As a result, landowners often manage their land to make it unattractive to the woodpeckers by harvesting pines before they reach old-growth stages, replacing longleaf pine with shortleaf pine, suppressing fires, and letting the understory grow. For example, in the town of Boiling Spring Lakes, North Carolina, red-cockaded woodpeckers were beginning to move back into an area of longleaf pine woodland that was being reviewed by the Fish and Wildlife Service as designation for critical habitat. During the injunction period, many of the individual trees that had been identified as “candidate trees” for red-cockaded woodpecker nesting mysteriously disappeared (Rawlins 2006).

Actions like those in Boiling Spring Lakes arise from rational economic behavior and from the landowners’ fear of the ESA’s prohibition against the “taking” of any endangered species. Historically, ***taking*** meant hunting, fishing, collecting, or trapping a creature to kill it or bring it into personal possession. The ESA’s definition of *taking* is much broader. In the ESA, *taking* includes any act that harms or harasses the protected creature in any way, intentional or not. Thus, as Bean et al. (1991) note in their analysis of landowners’ conflicts with the ESA, “a landowner whose bulldozers crush the larvae of an endangered butterfly on his land commits just as much of a taking as a hunter who deliberately shoots a bald eagle.”

This view of “taking” has significant implications for landowners. If a landowner inadvertently harms a member of the endangered species through normal land-use activities such as farming, logging, or development, criminal prosecution can result. It is this discouraging prospect that leads many landowners to deliberately alter habitat on their land. If an endangered species does inhabit their property, private landowners may resort to the strategy of the Three S’s – “shoot, shovel, and shut up.” The long-term effect of the resulting behavior is a reduction in available habitat for already endangered animals. This example of the red-cockaded woodpecker demonstrates how even legislation designed to protect endangered species can have unintended adverse consequences if it fails to consider the interests of private landowners.

3.2.4.3. San Bruno Mountain and the Evolution of Habitat Conservation Planning

Struggles arising from conflicts of interest between private individuals and conservation efforts have repeatedly caused what former US Interior Secretary Bruce Babbitt has called “environmental train wrecks” (Kaiser 1997). Conflicts of this sort have occurred because early versions of the ESA did not define the concept of critical habitat well and did little to develop the idea of saving species through preserving habitats (Noss et al. 1997). The ESA did prohibit destruction of the habitat of endangered species, but in practice this has been difficult to enforce (Bean et al. 1991) and even overruled in court (Noss et al. 1997). To prevent continued loss of habitat for endangered species and reduce conflicts with private landowners the Clinton administration increasingly resorted to a mechanism known as the habitat conservation plan (HCP).

HCPs arose out of a 1982 amendment to the ESA that allowed the issuance of “incidental take” permits for endangered species. ***Incidental take*** was defined as take that is “incidental to, and not the purpose of, carrying out an otherwise lawful activity.” To be granted such a take permit, the applicant, whether corporate or individual, must first prepare and submit a conservation plan. The plan must explain what the effects of the taking will be on the endangered species, how the effects will be mitigated, and how the species will benefit. Now called habitat conservation planning, this procedure was patterned after the resolution of an environmental/economic conflict over the proposed development of San Bruno Mountain near San Francisco, California.

San Bruno Mountain, attractive as a site for upper-class residential and commercial development, also represented some of the last undisturbed mountain habitat in the San Francisco Bay area and was the home of two endangered species of butterflies (Lehman 1995). Rather than resorting to litigation, the parties involved in the controversy devised a series of agreements that allowed for development of one-fifth of the mountain, but protected the remaining 80%, and 90% of the butterflies’ habitat.

Congress was so impressed with the San Bruno example that it codified it in a 1982 ESA amendment so that HCPs would “encourage creative partnerships between public and private sectors and among government agencies in the interests of species and habitat conservation” (Lehman 1995). The process was intended to foster resolution through negotiation, compromise, and recognition of the interests of all participants.

Supporters of HCPs maintain that this approach involves all vested interests and focuses on protecting the highest-quality and most productive habitats (Lehman 1995). Critics claim that the plans have inadequate scientific guidance, permit landowners to destroy habitat later if they enhance it initially (Kaiser 1997), provide few or no opportunities for public participation in formulating the plans, and have ineffective management provisions and poor oversight of plan implementation (O’Connell 1997). Furthermore, most HCPs are for single areas, species, and landowners and critics argue that this approach is overly narrow, restricted, and fragmented (O’Connell 1997).

Despite these criticisms, officials in the Clinton administration continued to work to make HCPs more attractive to landowners. In 1994, the US Department of Interior and the Department of Commerce issued a new policy entitled “No Surprises: Assuring Certainty for Private Landowners in Endangered Species Act Conservation Planning.” This revision, known as the “No-Surprises” policy, requires the responsible federal agency to provide landowners with assurances that they are not responsible for species protection if unforeseen circumstances arise (Walley 1996; Schilling 1997). Under this policy, after an HCP is approved, federal agencies cannot require any additional mitigation measures from a landowner to conserve an endangered species unless the agencies demonstrate “extraordinary circumstances” that warrant increased protection.

The no-surprises policy was intended to increase landowner cooperation and make the protection of endangered species more effective, but critics were quick to attack it. One hundred sixty-four scientists, including many of the world's leading conservation biologists, wrote letters protesting the policy to members of the US House Committee on Resources (Walley 1996). Their greatest concern was that there will be many surprises, rather than no surprises, in conservation planning. Because uncertainty and change are intrinsic to ecological systems, the policy unreasonably and unfairly restricts the ability of agencies to change conservation plans and adapt to changing conditions. The policy also has been criticized because it guarantees no surprises to the landowner as an inherent right, rather than as a privilege earned through proper conservation planning. According to the policy, the no-surprises assurance must be given to all landowners whether or not they make conservation commitments (Walley 1996).

Criticisms of the increased emphasis on HCPs have led to increased scrutiny of individual plans by conservation biologists. A comprehensive review of 44 HCPs, covering a range of land areas, locations, and landowner categories, gave mostly favorable reviews to the HCPs examined (Mann and Plummer 1997). Most of the plans were judged to have reliably determined the health of the species' population before being implemented. About half were judged to have made a reasonable prediction about the harm the landowners would cause species, and to have correctly determined the key threats to the species (Mann and Plummer 1997). Although the overall review was favorable, there were problems. Most plans did not do a good job determining how the HCP would affect species viability (not just the local population), provide for monitoring, or include basic natural-history data on species affected (Mann and Plummer 1997).

Limitations of HCPs have led to attempts to improve this approach. Increasingly, HCPs are supplemented with "no-take" management plans implemented via memoranda of agreement (MOA) and so-called ***safe harbor*** cooperative agreements (Costa 1997). MOA are agreements between a federal agency (usually the FWS) and a corporate landowner outlining conservation actions that the landowner can take to meet or exceed requirements of the ESA for habitat protection. For example, landowners can satisfy their ESA obligations by monitoring populations, managing and retaining current and future nesting habitat, producing and maintaining foraging habitat, conducting cooperative research, education and outreach, and letting the managed population provide donors for other populations (Costa 1997). One of the first agreements was signed in 1992 by the Georgia-Pacific Corporation (a lumber company) and the FWS to preserve habitat for the previously discussed red-cockaded woodpecker. By 1997, this MOA was protecting more than 66,000 acres of forest for the woodpecker (Costa 1997).

Safe harbor agreements are contracts under which a landowner agrees to actively maintain suitable habitat ("safe harbor") for a predetermined number of a species equal to the number present on the site when the agreement was formulated. In return, the landowner receives an incidental take permit that authorizes future land-use changes or management on other parts of the site that may be occupied by additional individuals of the endangered species. The major benefit of the safe harbor agreement is that it provides direct habitat improvement and maintenance for all the individuals or population subunits that are enrolled in the original conservation agreement. Once again, the first example of the use of a safe harbor agreement was for protection of the red-cockaded woodpecker. An initial agreement in 1995 in the Sandhills Region of south-central North Carolina succeeded in enrolling 24 landowners and more than 21,000 acres of habitat to be actively managed for the woodpecker. This acreage originally supported 46 woodpecker groups, but is estimated to be able to support up to 107 groups (Costa 1997). The agreement was endorsed by the landowners because it is based on initial numbers of woodpeckers present on a landowner's property at the time of enrollment. The landowner agrees to manage and monitor the habitat to maintain those numbers, but additional woodpeckers moving onto the property may be "taken."

Despite their imperfections, conservation approaches like HCPs, MOA, and safe harbor agreements acknowledge fundamental truths about the future of conservation. First, habitats must be conserved if species are to be conserved, and secondly, habitat and species conservation cannot be successful in the long run if they are restricted entirely to public land or to private reserves established by conservation organizations. Habitat and species conservation can be successful in a landscape context only if private landowners are involved and motivated partners. These realities reveal that efforts of greater landscape scale are needed to preserve populations and their habitats. It is far easier and more cost effective to protect intact ecosystems and the species they contain than to initiate emergency measures for critically endangered populations on degraded habitat.

POINTS OF ENGAGEMENT – QUESTION 2

Is it reasonable to expect "no surprises" in a conservation plan? If not, what could a responsible federal agency do to make the possibility of "surprises" acceptable to a landowner in negotiating a habitat conservation plan?

3.2.4.4. Criticisms of the Endangered Species Act

Beyond criticisms of habitat conservation plans, the ESA itself faced mounting criticism in the 1990s. Complaints from private business and development interests are chronic and predictable, but the ESA also has been increasingly subjected to substantive criticisms from conservation biologists. Many biologists have argued that instead of focusing on individual species, a more appropriate conservation goal is conservation of overall biodiversity and the management and protection of critical habitats and ecosystems (Rohlf 1991). Such critics contend that a narrow, single-species approach is slow, unwieldy, ignorant of the dynamics of real ecosystems, and wasteful of resources and efforts that could benefit multiple populations in the same habitat or ecosystem (Flather et al. 1998). One constructive response to this criticism is habitat- and regional-level analysis of endangered species' distributions, and development of strategies to promote the recovery of multiple species in the same habitat or region (Flather et al. 1998). Other biologically-based criticisms of the ESA include complaints that the law lacks defined thresholds to delineate endangered, threatened, and recovered species; that it does not adequately protect patchily distributed populations ("metapopulations"); that it does not protect habitat reserves sufficiently to sustain recovered populations; and that uncertain or long-term threats to endangered populations are discounted (Rohlf 1991).

Perhaps the most substantive biological criticism of the ESA is that it is reactive rather than proactive, responding only to the needs of species on the brink of extinction (Karr 1995). The reactive nature of the ESA also corrupts the listing process. Although listing is primarily the responsibility of the FWS and the National Marine Fisheries Service, many recent listings have been the products of lawsuits from environmental groups against the FWS over the failure to list particular species. Lawsuits are expensive to combat, and drain money in the endangered species program budget that was intended to acquire habitat and monitor endangered populations. In 2000, the FWS spent its entire budget for the listing and recovery of endangered species on legal fees. Thus, in 2001 the Bush administration proposed new regulations that would have severely limited, for 1 year, the power of environmental groups to bring lawsuits against the FWS over endangered species. That proposal ignited new criticism that the administration was attempting to squash efforts to protect endangered species.

The ESA also has been criticized for alleged ineffectiveness. In its 2003–2004 report to the US Congress, the US Fish and Wildlife Service could name only 35 delistings of species since the Act's inception. Of these, only 12 were due to actual recovery. Fourteen species were delisted because of new information, taxonomic revision, or administrative reasons, and nine were delisted because they became extinct under the Act's "protection" (U S Fish and Wildlife Service 2004), resulting in a net final score of only +3 in terms of recoveries to extinctions.

Despite the ESA's shortcomings, it is difficult even for critics to imagine what sort of legislation could replace or improve upon its fundamental legislative virtues. More than any other statute, the ESA affirms that species have intrinsic value, and US courts have interpreted the ESA to give protection to any species listed as "endangered" by the ESA regardless of the economic cost of protection (Rohlf 1995). The ESA also clearly and explicitly extends legal rights to non-human species (Karr 1995). The US environmental historian Joseph Petulla described the ESA as one of the most remarkable, radical, and original laws ever passed because, through its protection, "a listed non-human resident of the United States is guaranteed, in a special sense, life and liberty" (Petulla 1977). Overall, the ESA has performed well at the functional level, and there is general agreement that fewer extinctions have occurred under the ESA than would have without it (Committee on Scientific Issues in the Endangered Species Act 1995).

Besieged by controversy, fraught with limitations, and plagued by well-publicized failures, the ESA nevertheless has been instrumental in preserving many species, albeit often at small population sizes. The ESA has operated in the courts more efficiently than many other legal attempts to preserve biodiversity because it contains easily defined concepts and goals. In particular, the "species" concept, the cornerstone of the ESA's validity, has proved more definable and defensible in legal circles than have concepts such as "biodiversity," "habitat," or "ecosystem" (Karr 1995). Perhaps most importantly, the ESA remains an important legislative model for efforts to save species worldwide.

3.2.5. Water as an Inalienable Reserve – South Africa and Australia Establish Radical Categories for Conservation Law

Democratically elected governments derive much of their authority and legitimacy from the view that such governments hold certain rights and entitlements in trust for the people and are therefore obligated to protect those rights for the common good. This is known in the legal community as the doctrine of ***public trust***, which can be traced to the Roman Emperor Justinian, who, in AD 533, assembled all of Roman law in a single work, the Institutes of Justinian. Among these, he included this principle, quoted at the head of this chapter, "By the law of nature, these things are common to mankind – the air, running water, the sea, and consequently the shores of the sea" (Justinian 1997:167). This doctrine of the public trust, which has become one of the most important foundations of national environmental laws throughout the world, is perhaps nowhere more important than in the management and conservation of freshwater resources and the aquatic habitats that depend upon them. Drawing on this principle, the Republic of South Africa has established a radical conservation concept, the water allocation principle known as the "Reserve" in their National Water Act of 1998. Established by this law, the Reserve concept controls water allocation according to two principles. First, the government shall maintain a “lifeline” allocation of water sufficient to meet the basic needs of South Africans for drinking, cooking, sanitation, and other essential and personal purposes. Second, the government shall maintain an allocation of water sufficient to support ecosystem functions (aquatic and otherwise) in order to preserve native biodiversity and secure for the common good the services provided by such functions. These allocations have priority over all other uses (Postel and Richter 2003).

At first glance, such a law hardly looks like a controversial or radical endorsement of conservation. Shouldn’t everyone have water for drinking and washing, and shouldn’t we expect that the government will ensure that the streams and lakes will have fish and the wetlands will have frogs and toads? In fact, however, most western governments, including most European countries and the United States, make no such constitutional guarantees, and water demands of agriculture and industry often diminish allocations to individuals and for ecosystem functions. In South Africa, the Reserve concept forces all other uses of water into secondary, non-essential categories, such that any requested use of water that is not for personal sustenance and health or that is not directly related to preserving ecosystem function must be approved and licensed by the government. We can see the outcomes and implications of this concept emerge as we look at them systematically in Table 3.1. It is fair to say that, for the conservation of freshwater aquatic habitats, the Reserve concept changes everything. The concept was so compelling that the World Conservation Union (IUCN) adopted it in principle for its master plan of water and aquatic habitat conservation for the twenty-first century, Vision for Water and Nature: A World Strategy for Conservation and Sustainable Management of Water Resources in the Twenty-first Century (IUCN 2000). And the idea is spreading.

It is not surprising that a new view of water conservation law should arise in a country like South Africa, a dry land where water is a precious commodity. Similarly, in Australia, the driest inhabited continent on Earth, another new concept for water conservation has emerged in the Council of Australian Governments Water Reform Framework of 1994, which calls for sustainability in water use and protection for freshwater ecosystems. Such a legal perspective has stimulated the development of a “cap” on water allocations in one of Australia’s largest and most well-known river systems, the Murray-Darling Basin, in which a limit has been placed on water allocations to create a flow regime designed to protect the river’s health. Environmental policy analysts Sandra Postel and Brian Richter also note that the Murray-Darling cap is a way to guard against “the ‘tyranny of small decisions,’ – the large cumulative impact caused by numerous small river diversions or hydrologic alterations that individually would not raise much concern.… To our knowledge, the [Murray-Darling] cap is the only serious attempt in the world … to limit extractions from a large multi-state river basin that is already oversubscribed” (Postel and Richter 2003:92). The “oversubscribed” condition is telling, and most experts, while commending the intent, are convinced that the present cap limiting allocations still allows too much withdrawal to restore the full ecosystem functioning of the Murray-Darling system. But it is a beginning.

Although the US has no constitutional concept of a water “Reserve” like the Republic of South Africa, it does have a well-established legal precedent of “reserved water rights” for federally reserved lands. The concept of reserved water rights arose with regard to a case, *Winters v. United States*, involving a dispute between private water users and two Indian tribes on a reservation in Montana in 1908, with the tribes claiming that private users outside the reservation were not leaving enough water for use on the reservation. In this case, the US Supreme Court ruled

TABLE 3.1. Water allocations and their implications under South Africa’s National Water Act.

Water Allocation	Purpose of Water		End Objective	Mode of Allocation
Water for Basic Human Needs	To support basic human needs (i.e., drinking water, cooking, and sanitation)		Meet human survival needs	Nonnegotiable
Water for the Ecological Reserve	To sustain a certain state of the ecosystem associated with a specific range of goods and services (e.g. subsistence fishing and recreation)	Use of goods and services support a range of benefits	Social and economic growth and well-being	Negotiated through ongoing stakeholder dialogue and consensus around trade-offs
Water for Licensed Use	To support activities that rely on water as applied outside of the ecosystem (e.g., irrigation)	Activities lead to a range of benefits	Social and economic growth and well-being	Negotiated through ongoing stakeholder dialogue and consensus around trade-offs

Source: Postel and Richter (2003). From *Rivers for Life*. Copyright 2003 by Island Press. Reproduced by permission of Island Press, Washington, DC.

that in establishing the reservation, the US government had "impliedly" reserved for the tribes enough water to carry out the purposes for which the reservation was created. The precedent set in *Winter* has been more recently extended to any federal land reservations, not just Indian land. US law now recognizes that any federally reserved land can claim reserved water rights to the extent those rights are necessary to carry out the purposes for which the reservation was established, and the priority date for rights is not from when rights are first claimed, but from the date the reservation was established. This means that entities like national parks, forests, and wildlife refuges could, in theory, claim rights to water to the extent necessary to carry out the purpose for which their reservation was created. Unfortunately for conservation interests, this right is rarely asserted, and, when asserted, the agency representing the reservation has rarely won in court (Postel and Richter 2003).

3.3. International Conservation Law: Concept and Development

3.3.1. General Considerations

Today conservation is an international effort involving all modern nation states to varying degrees. Although modern international conservation law does, in some cases, implicitly recognize the intrinsic value of the species and habitats it preserves, it is primarily driven by the utilitarian interests we have already noted, and by the equalization of risks, usually in the form of increased mutual international interdependence and increased concern for transgenerational equity, a concept which we will examine later in more detail. Modern efforts in international conservation law arise from one or more of the following sources: (1) bilateral or multilateral treaties among nations, (2) binding acts of international organizations, (3) rules of customary international law, and (4) judgments of an international court or tribunal (Sands 1999:122). As we analyze the development of international and national conservation law in the following examples, observe how these frameworks of conservation law are employed.

3.3.2. A Forum for Cooperation and Legal Foundation – The United Nations and Its Environmental Programs

3.3.2.1. Background and Context

Today the agents that broker international conservation initiative and multinational agreements are the United Nations (UN) and, within the UN, its Environmental Programme (UNEP). Largely through the impetus of UNEP and other UN environmental programs, modern nation-states have entered into over 250 treaties, conventions, and agreements focusing on international conservation during the last 30 years, and today over 1,000 international legal instruments, most of them binding, contain at least one section or provision that addresses environmental conservation. In addition to stimulating the formation of new regional international organizations and encouraging their work in conservation legislation, UNEP and other UN programs, by specifying international conservation priorities, often have directly stimulated the development of international conservation agreements among nations in the same region, serving as a catalyst for more coordinated regional action for environmental conservation. For example, since the Stockholm Conference of 1972, the European Union (EU) has enacted more than 200 items of environmental legislation that govern the western European community. Similarly, the international attention, communication, and cooperation provided by the UN and its program have inspired the development of a multitude of regional multilaterial organizations, many of which have been instrumental in developing regional international treaties for conservation. Perhaps the most advanced of these has been the European Union (EU), which legal scholar Joseph DiMento described as "unmatched as a manifestation of international law in both its substantive and procedural content" (DiMento 2003:26). In fact, the Amsterdam Treaty of the EU requires that environmental protection be integrated into all EU policies and activities (Vig and Axelrod 1999:16).

Perhaps the UN's greatest initial contribution to the world conservation effort has been that it provided a forum for the discussion of international conservation issues and a general means to permit adoption of international conservation agreements. However, for the first 2 decades of its existence, such efforts were often *ad hoc* and largely uncoordinated. A turning point in international conservation came in 1972, with the convening of the United Nations Conference on the Global Environment in Stockholm, Sweden, better known as the Stockholm Conference.

3.3.2.2. Stockholm: The Beginnings of Modern International Conservation Law

Most legal scholars today mark the beginnings of coordinated international environmental and conservation law with the convening of the Stockholm Conference of 1972 (DiMento 2003:18). The expressed purpose of the Stockholm Conference was to provide a framework within which the UN could comprehensively assess the problems of the human environment and place the focus of national governments and the public on such problems. Its most significant achievement was the production of the Declaration on the Human Environment, a document containing 26 principles and 109 recommendations related to environmental protection and conservation. Perhaps even more importantly, it was at Stockholm that the UN created its first specifically environmental agency, the aforementioned United Nations Environmental Programme. UNEP was charged with the responsibility for creating both new international conventions to foster conservation and protect the environment, as well as the responsibility for their enforcement.

The Stockholm Conference was significant in that the United Nations became involved in world conservation in comprehensive and systematic ways, something it had rarely done before. UNEP made environmental concerns and programs a permanent fixture of the United Nations agenda. For the first time, a global institution created a series of global programs designed to address environmental and conservation concerns.

The creation of UNEP had an almost immediate impact on world conservation. In 1973, just 1 year after Stockholm, UNEP's Governing Board declared regional seas to be an important conservation priority. This emphasis lead directly to the development the Barcelona Convention of 1976 for the Protection of the Mediterranean Sea Against Pollution, an agreement developed by Mediterranean nations that sought to reduce pollution and preserve native Mediterranean Sea species (DiMento 2003:28). The Barcelona Convention provided the incentive and model for regional environmental and conservation treaties that would follow during the next 30 years, with regional treaties developed for most of the world's oceans from 1972 to 1986. By 1988, more than 100 nations and 50 international organizations were cooperating in regional seas programs (Sand 1988) and the number has continued to increase. In addition to regional conventions and protocols, the 1982 Montego Bay Convention, developed in association with the Third United Nations Conference on the Law of the Sea, addressed major issues of ocean conservation on a worldwide basis. As such conventions have developed, the most important trend has been a shift from use-oriented to resource-oriented approaches. The use-oriented approach emphasized navigation and fishing. The resource-oriented approach emphasizes sustainable development and harvest of ocean resources, focusing on defining and enforcing standards of "protection," "conservation," "management," and "development" (Sand 1988).

Although the programs, treaties, and conventions that grew out of the Stockholm Conference were critical to world conservation, most did not deal directly with the problems of endangered species or the preservation of world biodiversity. The most important international agreement on this issue, The Convention on International Trade in Endangered Species of Wild Flora and Fauna of 1973 (CITES), grew out of the combined efforts of the International Union for the Conservation of Nature (IUCN), and UNEP.

3.3.2.3. Protection of Endangered Species: The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)

The Convention on International Trade in Endangered Species of Wild Fauna and Flora of 1973 (CITES) is arguably the most important international conservation agreement operating today, because it specifically regulates or prohibits commercial trade in globally endangered species or their products. Although the United States had passed an Endangered Species Act in 1966, the concept, much less protection, of endangered species was still largely unknown as an issue of international relations and global politics before 1970.

In 1950, supported by great encouragement and a tiny grant (US$2,500) from the United Nations Educational, Scientific, and Cultural Organization (UNESCO), IUCN began a program it called the Survival Service, a unit within the organization that began making lists and short status reports of endangered and threatened species worldwide (Chapter 1). These reports, which by the 1960s were becoming published as the now famous "Red Data Books," ultimately became the most important source and most respected authority for identifying the world's endangered species and their status (www.iucnredlist.org). Using relatively simple decision rules as criteria, the Red List categorizes species according to their relative endangerment (Figure 3.4). By drawing the attention of the international community to the plight of endangered species, IUCN's reports began to spur debate in the UN. As early as 1963, the directors of UNEP called for "an international Convention on regulations of export, transit, and import of rare or threatened wildlife species or their skins or trophies" (Holdgate 1999:114). Various drafts circulated from 1964 to 1972, but none could bring consensus. Finally, in 1973, an intergovernmental negotiating conference was convened in Washington, DC. A formal agreement was reached, and a text of CITES was prepared and circulated in three languages (Holdgate 1999:115).

From this point, support for CITES built steadily, and the Convention went into force in 1975. Although a great achievement in international negotiation, CITES is an imperfect document, achieving much of its consensus by being deliberately vague on its most important points. There has always been disagreement, fueled in part by the treaty's own ambiguous language, as to whether CITES is an instrument for wildlife protection or a means to regulate wildlife trade. CITES does not protect all wildlife, but only "tradable" wildlife and wildlife products that are bought or sold in transactions involving two or more countries. In fact, the heart of the CITES treaty is found not in the main body of the document, but in three appendices that list categories of species regulated under the terms of the treaty. Appendix I lists species that are endangered and vulnerable to existing or

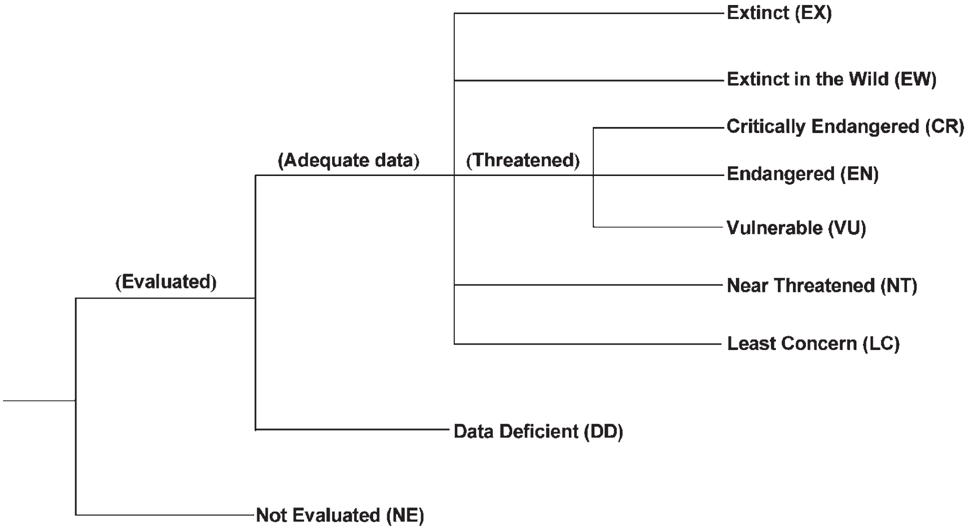

FIGURE 3.4. Categorization of species under the IUCN Red List. Using a set of decision rules as a classification algorithm, the IUCN assigns a categorical status to Red List species intended to reflect their risk of endangerment. (Courtesy of John Kidd, IUCN.)

potential trade. Commercial trade in Appendix I species is prohibited, and permits from both the importing and exporting country must be obtained even for non-commercial transport. Appendix II species are those that either could be threatened by large volumes of trade or that cannot be distinguished from a threatened species. Trade involving species in these categories requires a permit from the exporting country. Appendix III species are not globally endangered, but may be listed at the initiative of an individual state seeking international cooperation for that species' protection. In Appendix III species, nations are asked not to permit importation of the species without an export permit from the listing country. Parties to the treaty meet every 2 years to make amendments to the appendices and develop new species and animal products' lists and identification manuals to improve enforcement (Slocombe 1989).

CITES has proved to be an evolving document, and amendments to original provisions are not uncommon, reflecting changes in perceptions among delegates about the best way to achieve conservation of wildlife. Originally a treaty that equated conservation with strict protectionism in international trade, more recent meetings of CITES participants have shown a growing tendency to permit some trade in formerly protected species if it can be shown that such trade actually enhances their conservation. Thus, attempts to apply CITES to specific conservation dilemmas often have proved problematic. For example, in November 1994 CITES delegates agreed to allow trade in live southern white rhinos from the Republic of South Africa, an action based primarily on the success of rhino conservation programs in that country that had restored a population of 20 individuals (all that remained in the country by 1920) to about 6,300, the largest national population in Africa (Kelso 1995). Sales of white rhino are actually expected to improve the status of the species in South Africa because proceeds would be spent on further rhino conservation efforts. The rhinos that are sold to other governments were expected to aid in restoring rhino populations currently in decline in other countries.

The same meeting also repealed the 1987 mandate to destroy existing stockpiles of rhino horns, previously sold on the world market as raw material for medicines, aphrodisiacs and, in some Middle Eastern countries, as handles for ceremonial daggers. Although the original mandate was justified as a means to eliminate incentives for national governments to trade in rhino horn products and thus discourage poaching, more recent delegate opinion was that destruction of stockpiles would cause the price of rhino horn to increase, escalating poaching pressure (Kelso 1995). Governments now have been asked to "identify, mark, and secure" their rhino horns in national stockpiles that have, ironically, grown because of increasingly effective enforcement of conservation laws, leading to seizures of rhino horns taken by poachers. Although this meeting did not actually approve the sale or trade of horns in such stockpiles, it paved the way to do so at a later time, under strict controls, if current inventory can be carefully marked. CITES, and the standards for species protection that it expressed, also has had practical and substantive implications in international relations. In April 1994, the Clinton administration of the US government imposed trade sanctions on Taiwan after that government failed to curtail trade in rhinoceros and tiger parts despite warnings from the United States. Some scholars mark this action as the first time in history that international trade sanctions had been used directly to protect wildlife (Coggins 2003:5).

With the increasing effectiveness of international mechanisms to create agreements promoting conservation, the international community was ready to take its next step: the integration of conservation with the problems of human poverty and development. This was the subject of the United Nations Conference on Environment and Development in Rio de Janiero, Brazil in 1992, better known as the Rio Summit.

3.3.2.4. Rio 1992 – Combining Conservation and Economics in International Agreements

In June 1992, there were in fact two major global environmental conferences held in Rio De Janiero, Brazil. Together, they produced a number of environmental documents signed by most or, in some cases, all of the participating nations. The United Nations Conference on Environment and Development (UNCED), popularly referred to as the Rio Summit or Earth Summit, was a formal conference of official government delegations. Simultaneously, a large gathering of non-governmental organizations gathered for the Global Forum, a mixture of NGO networking, street shows, trade fairs, and environmental demonstrations (Parson et al. 1992).

The explicit aim of the Rio Summit was to integrate efforts to protect planetary ecosystems with economic development of the poor nations of the world. To that end it produced five documents. The best known of these is the Rio Declaration, originally conceived as a kind of "Earth Charter" that summarized international consensus on environmental policy and development. The Rio Declaration, signed by all participating nations, affirms environmental protection as an integral part of development.

The *Framework Convention on Climate Change* primarily addresses emissions limits and standards of "greenhouse gases" associated with fossil fuels. Although the convention does not set specific targets, its ambitious objective was the "stabilization of greenhouse gas concentrations in the atmosphere that would prevent dangerous anthropogenic interference with the climate system … within a time frame sufficient to allow ecosystems to adapt naturally" (United Nations Framework Convention on Climate Change 1992). Representatives of 153 countries signed this convention, which eventually resulted in negotiation of the Kyoto Protocol.

The *Convention to Combat Desertification* was established to reduce the process of desertification, mainly by adopting measures to protect dryland environments and improving the living standards of people who use them through improving livestock and forestry practices, land use reform, soil and water conservation, and wildlife protection. To date, over 130 countries have now ratified this convention and submitted plans on how they plan to combat desertification within their own borders. However, lack of funding has made progress toward this convention's goals difficult.

The *Statement on Forest Principles* was a non-binding declaration that pledged its signers to keep 17 principles "under assessment for their adequacy with regard to further international cooperation on forest issues" (Parson et al. 1992). Progress toward a formal treaty on forests at the Rio Summit failed primarily because of differences between industrialized countries that wanted a treaty focusing on tropical forests, and developing countries that wanted a treaty including boreal and temperate forests.

The *Convention on Biological Diversity* (CBD) addressed conservation and sustainable use of biodiversity along with fair sharing of genetic resources. The 153 signers pledged to develop plans to protect habitats and species, provide funds and technology to assist developing countries to provide protection, ensure commercial access to biological resources for development, share revenues fairly among sources and developers, establish safety regulations, and accept liability for risks associated with biotechnology development (Parson et al. 1992). Entering into force only 18 months later on December 29, 1993, 175 nations had signed on by 2001, and most of the major provisions of the CBD are now being implemented.

The most comprehensive document signed at the Rio Summit was *Agenda 21*, an 800-page "work plan" addressing social and economic dimensions of environment and development, conservation and management of resources, and means of implementation. Agenda 21's structure was based on key environmental and conservation issues, including the problems of desertification, protecting the atmosphere, and managing toxic wastes. It also addressed social issues with environmental dimensions such as poverty and technology transfer (Greene 1994). Overall, Agenda 21 identified priority environmental issues and divided them into two categories: the priority needs for environmental protection, including atmospheric protection and climate change, protection of land resources, halting deforestation, conserving biodiversity and protecting freshwater and saltwater resources, and the problems of human industry and technology that pose particular threats to the environment, including threats posed from biotechnology, hazardous wastes, sewage and agriculture (Sands 1999).

In its social and economic dimensions, Agenda 21 affirmed the need to eradicate poverty and hunger, to manage resources sustainably, to link human health to environmental and socioeconomic improvements and to integrate environmental factors into policymaking, law, economics and national accounting. In addressing conservation and management of resources for development, Agenda 21 supported allocation of land that provided the greatest sustainable benefits. It affirmed the need for worldwide conservation of biodiversity, proper management of mountain resources, more information on mountain ecosystems, and integrated development of mountain watersheds. In this section, Agenda 21 also affirmed the importance of freshwater resources, provision of safe drinking water, and the need for safe management of various kinds of toxic chemicals and hazardous wastes. In its final section on means of implementation, Agenda 21 supported promoting public awareness, establishing a new UN body, the Sustainable Development Commission (SDC), to coordinate pursuit of sustainable development among international organizations and monitor progress by governments and international organizations toward reaching the goals set out in the Agenda. It concludes with a discussion of the importance of collecting and using information for sustainable development and for implementing Agenda 21 (Parson et al. 1992). Agenda 21 spurred controversy and failed to reach agreement on issues of fish stocks, targets and deadlines for increases in development assistance, and the governance of the Global Environmental Facility (GEF), among others (Parson et al. 1992).

A significant shortcoming of Agenda 21 has been its failure to establish new regimes of international development, particularly to benefit poorer countries, including specific sets of rules and practices that would define roles and create shared expectations in the international community for such development, along with the institutions needed to implement such practices. Despite these and other shortcomings, Agenda 21 has profoundly influenced international conservation law and policy. Although not all are legally binding, the principles of Agenda 21 have already found their way into many UN resolutions; the conventions on climate change and biodiversity have increasingly set the standard of international policy, practice, and expectation on the issues they address. The Rio Declaration, although controversial, continues to contribute to common goals and standards of national behavior informed by environmental principles.

3.4. The Process: Creating and Enforcing International Conservation Law

If international conservation law consisted merely of value-neutral rules, its most important element would be ***hard law***, formal conventions and treaties adopted by many nations, with explicit mechanisms for enforcement. However, the actual behavior of the modern international community has demonstrated the growing importance of ***soft law***, nonbinding agreements that, although having no official means of enforcement, eventually come to define the norms and standards for international behavior. The reality of this concept can be seen in the way in which international laws on environmental conservation actually come into being.

In 1977 UNEP established a Working Group of Experts on Environmental Law, whose recommendations were endorsed by the UNEP governing council and, in 1982, by the UN General Assembly. Although individual nations were not legally bound to use these guidelines, much of the so-called "soft law" recommendations from this panel of experts and other sources has become, over time, an increasingly recognized international standard (Sand 1988). Such soft law agreements are often the sources for developing the actual wording of "hard law" agreements in more formal conventions, and generally create a climate of compliance by establishing a normative standard that makes them as effective as hard law. As legal scholar Jane Roberts observed, these agreements often create such a spirit of shared values and goals that in terms of international behavior, they "have a predictive value similar to those expressed in hard law" (Roberts 2004:103).

Even soft laws in conservation must have a catalyst. Although every international convention, treaty, or protocol is a product of unique circumstances, the development of international instruments in conservation usually follows a four-step process: (1) issue definition; (2) fact finding; (3) creation of an international body or regime to address the problem; and (4) consolidation and strengthening the regime.

For increased clarity and understanding, certain concepts repeatedly invoked in international conservation law require careful definition. Once conceived and defined, laws must find a mechanism of ***implementation***, that is, nations must take specific actions to make international treaties operational in their own national legal system. The purpose of creating mechanisms of implementation is to increase ***compliance***, that is, to increase the extent to which the behavior of a state, as a party to an international treaty, actually conforms to the conditions of the treaty (Faure and Lefevere 1999:139). Methods used to force states to first implement and then comply with international agreements are mechanisms of ***enforcement***, and vary with individual agreements and conditions. The goal of such enforcement is ultimately ***effectiveness***, a measure, not simply of whether the nation lives up to the conditions of the treaty, but of whether such behavior actually achieves the objectives stated in the treaty. Thus, an ideal international conservation agreement is one in which there are clear and feasible mechanisms of implementation, high levels of compliance, and workable methods of enforcement, all leading to accomplishing the goals for which the agreement was formed in the first place (high effectiveness). Regrettably, not every international conservation treaty or convention gains high marks in all areas.

Weiss and Jacobson (1999) developed a conceptual model, based on the actual success of a variety of international environmental agreements, to show how various factors affect implementation, compliance and effectiveness of international conservation treaties (Figure 3.5). Compliance with international treaties is affected by the characteristics of the activity (for example, numbers of participants, characteristics of markets, location of the activity), characteristics of the agreement, and the state of

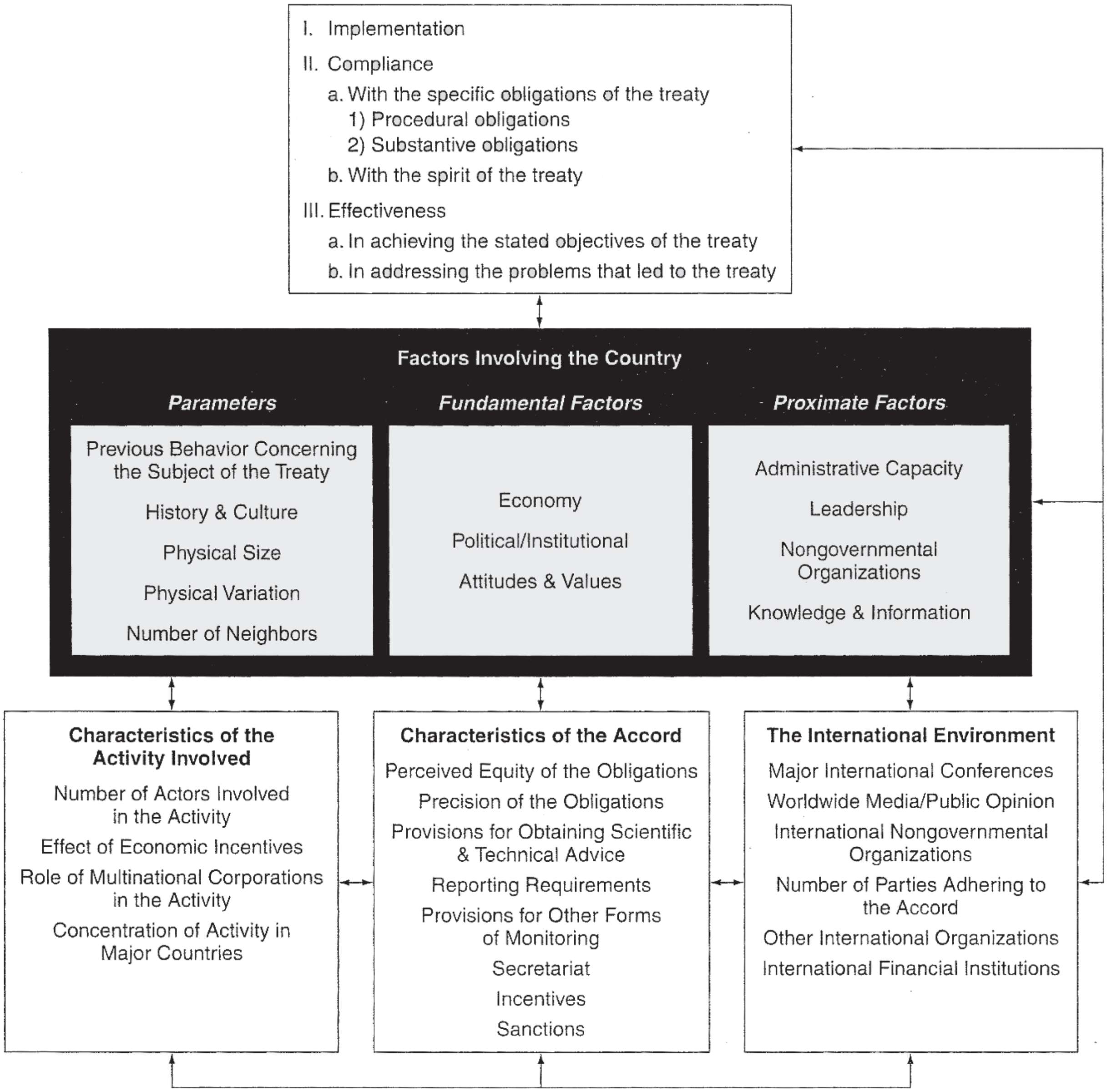

FIGURE 3.5. A model of factors that affect implementation, compliance and effectiveness of international treaties and conventions in conservation. Weiss et al. 1998, figure: 'Model of factors that affect implementation'. Copyright 1998 Massachusetts Institute of Technology. With permission of the MIT Press. Original re-design and enhancements by the McGraw-Hill Companies. Fred Van Dyke, Conservation Biology: Foundations, Concepts, Applications © 2003, McGraw-Hill, Reproduced with permission of the McGraw-Hill Companies.)

the international environment. A general trend has been that the smaller the number of participants involved in the activity, the easier the activity is to regulate internationally. Likewise, participants in an activity that dealt with large, global markets also were easier to regulate than participants in smaller firms and more local markets because global corporations and businesses were far more concerned about international image. The most important characteristic of the treaty or convention itself was equitability. Accords perceived by all parties to provide for fair treatment had much higher compliance than those that were perceived to favor some participants over others. International reception also plays an important role in compliance. The more persistently and publicly the international community focuses on a conservation problem, the more compliance with international conservation agreements related to that problem increases. In addition, the clear support of a "leader" country or group of countries, such as the United States or the European Union, for a particular accord also is a critical factor in the level of compliance. Where such leadership is present, international compliance is high.

Compliance is affected by both intent and capacity. *Intent*, or political will, can be judged from the behavior of national leaders and political bodies, and is a necessary but insufficient condition for compliance. With intent, the country also must possess the *capacity* to comply, requiring an efficient and honest environmental bureaucracy, economic resources, technical expertise and public support. Weiss and Jacobson have suggested three strategies for strengthening international compliance. The first of these is the ***sunshine approach*** which focuses on mechanisms to bring the behavior of key parties into the open for public scrutiny, including such actions as regular reporting, peer scrutiny, on site monitoring and media access and coverage. In this area, NGOs in conservation often play a critical role. In countries where NGOs are active in publicizing examples of non-compliance, the more likely they are to strengthen their government's intention to comply. Complementing Weiss and Jacobson's conclusions, international legal scholars Michael Faure and Jürgen Lefevere note that "the stronger and more active NGOs are with respect to the issue area of the treaty, the larger the probability of compliance" (Faure and Lefevere 1999:138). And the more actively both government and NGOs are engaged in reporting information relevant to the agreement, the more compliance increases. Secondly, this pattern of behavior instigates its own reinforcement because it encourages the development of ***compliance information systems*** that are built into government structures, systems whose aim is to ensure compliance and report non-compliance (Faure and Lefevere 1999:143). At the international level, the primary coordinating body for such compliance information systems is The Global Environmental Facility (GEF), established by The World Bank in 1991 in cooperation with UNEP and the United Nations Development Programme. To encourage compliance, GEF provides funding for the implementation of treaties that target various aspects of environmental quality and conservation. Finally, *positive incentives* work where a country has compliance intention but not capacity. Here, inputs of money, technical expertise, capital, training, or special considerations from other countries can increase compliance. UNESCO has instituted a number of programs to provide such incentives toward compliance, such as the World Heritage List (WHL) of sites of cultural and natural heritage. Administered by the World Heritage Centre in Paris, France, the WHL, a program created by the Convention Concerning the Protection of the World Cultural and Natural Heritage of 1972, is designed to identify and protect sites of outstanding cultural and natural value in every nation. In this case, the positive incentives take the form of providing help with administrative oversight, technical expertise, financial and material resources, and international influence for the designation and protection of listed sites. By 2007, the WHL had recognized (technically, "inscribed") 851 individual sites identified by 184 state parties as sites of particular cultural or natural value.

If the above mechanisms fail, ***coercive measures*** can be effective against parties that have capacity to comply but lack intention. Sanctions, penalties, loss of membership in international organizations or of privileges in international dealings can be effective in motivating unwilling parties to comply with agreements (Weiss and Jacobson 1999).

3.5. The Problem of Interdependence: How Does One Nation Promote Global Conservation without Negative Effects on Other Nations?

3.5.1. The Nature of International Legal Interdependence

Both international conservation law and the national laws of modern nation states have increased in breadth and matured in application in the last 3 decades. National law and international conventions are often aiming at the same goal, but there are many instances in which they run afoul of one another in the pursuit of conservation ideals. Although the worldwide trend in response to conservation treaties and conventions has been one of increasing compliance, factors affecting compliance are complex and national responses to international conservation efforts are not uniform. Increasingly, conservation efforts at international levels are guided, as well as constrained, by two overriding principles that often pull in opposite directions, both of which have important implications at national levels. The first is the increasing awareness and consensus that every nation has a responsibility to conserve its natural resources and must not damage them for use by future generations. This first principle is rooted in an axiom that has become even more foundational to international conservation: the commitment to intergenerational equity. Intergenerational equity is itself supported by three core ideas. First, each generation should be required to conserve the natural and cultural resource base of its own nation so that it does not restrict the options available to future generations in addressing their problems and achieving their goals. Second, each generation should maintain their environmental quality in such a state that it is in no worse condition than that which they received. Finally, members of every generation should have comparable rights of access to the legacy of past generations and should conserve this access for future generations. These are not empty concepts, but ones that increasingly influence how international law is expressed and implemented. In the Philippines, the Supreme Court recognized intergenerational equality by granting constitutional standing to a group of children to represent the interests of future generations in their efforts to stop the leasing of biologically diverse forests for development.

The second foundational concept of modern environmental law is that every nation has sovereign rights over its own national resources, and these rights are not to be infringed by other nations. Thus, competing claims of responsible conservation stewardship for the sake of intergenerational equity and national resource sovereignty by different nations can create problems for conservation initiatives. In a world of increasing global connection and dependence, initiatives for global conservation by a single nation must assess their effects upon other nations to be successful. Environmental policy scholar Edith Brown Weiss has noted, "In international environmental law, the most important development for the next century may be the emerging interaction of intergovernmental environmental law with transnational law …" (Weiss 1999:102). Further, Weiss perceives that "International law has always been linked with national law, for it is implemented through national, provincial, and local laws … national laws, independent of any treaty, provide protection to other countries or their citizens for harm that occurs within the country but injures those outside" (Weiss 1999:104). To better understand and appreciate the fascinating complexity of and connections between the claims of environmental protection and national sovereignty, national and international conservation law, and governments and non-governmental organizations, we consider the following examples of legislation designed to protect dolphins from tuna fishermen and sea turtles from shrimp trawlers.

3.5.2. Case History I: Tuna and Dolphins

In 1972, just 2 years after passage of the NEPA and only a year before passage of the amended Endangered Species Act, the US Congress enacted the Marine Mammal Protection Act (MMPA). The MMPA was a relatively minor and non-controversial piece of legislation that enjoyed broad bipartisan support. The Act's clear and simple goal was to protect "certain species and population stocks of marine mammals that are, or may be, in danger of extinction or depletion as a result of man's activities." One of the MMPA's mechanisms to achieve this goal was to reduce "incidental kill or serious injury of marine mammals … to insignificant levels approaching a zero mortality and serious injury rate."

The deaths of marine mammals associated with "incidental kill" had increasingly become a cause for scandal and condemnation by the public and the press, particularly in regard to the killing of dolphins by tuna fishermen. The problem had been developing since 1950s, when tuna fishermen began to employ purse-seine nets in capturing tuna. Such nets captured tuna in large schools when they fed near the surface. After tuna were surrounded by the purse-seine net, the bottom of the net was pulled together, trapping the tuna and all other organisms inside (Joyner and Tyler 2000).

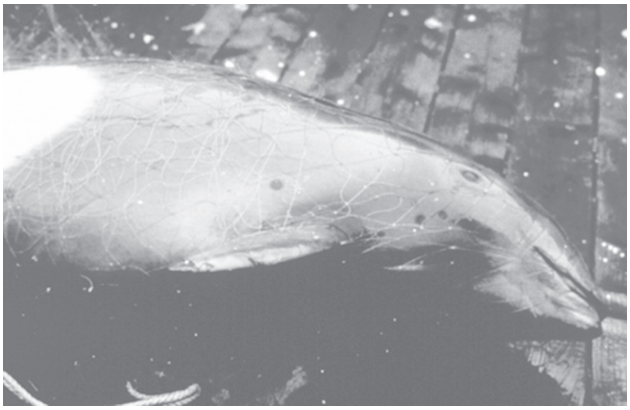

FIGURE 3.6. The Dall's porpoise (*Phocoenoides dalli*) is one of many species of porpoises and dolphins often killed as "bycatch" in the process of tuna fishing. The "incidental kill" of dolphins in association with tuna fishing has resulted in the deaths of millions of dolphins worldwide. (Photo courtesy of US National Marine Fisheries Service.)

Dolphins often travel directly above schools of tuna, so tuna fishermen began to track dolphins as an indicator of tuna presence. Thus, it was not surprising, or even "incidental," that dolphins were killed with tuna, either by drowning in the net or being crushed by the harvesting machinery. Since the 1960s, an estimated six million dolphins have perished in this manner (Figure 3.6).

By the late 1980s, US environmental and conservation NGOs successfully pressured the US Congress to add an amendment to the MMPA which established stringent guidelines for US tuna fishermen and all tuna fishing in the US waters to assure protection for dolphins and other species. It soon became apparent, however, that other countries, including those harvesting the majority of tuna, were not following standards set by the MMPA. To encourage adoption of such standards on an international level and to protect dolphin populations worldwide, the US Congress twice amended the MMPA. In 1984, the MMPA was altered to require an embargo on tuna imports from any country whose commercial fleets killed more dolphins than US fleets. In 1988, Congress added additional requirements for all tuna-exporting nations attempting to market tuna in the United States. Tuna-exporting countries were required to reduce incidental kill of non-tuna species to the level of US fishing fleets, and were prohibited from using large-scale drift nets, encircling marine mammals without direct evidence of the presence of tuna, or using purse-seine nets after sundown. The amendment also specified that failure to comply would lead the US Secretary of Commerce to ban imports of tuna from countries violating the regulation or from countries they sold tuna to (to prevent trans-national shipments as a way of getting around the regulation). In effect, this placed a US embargo on the tuna products of the offending nation. (Miller and Croston 1998; Joyner and Tyler 2000; Salzman and Thompson 2003:219).

3.5.3. Case History II: Shrimp and Sea Turtles

In 1989, the US Congress added a provision (Section 609) to Public Law 101–162 that became known as the "Sea Turtle Act" (Joyner and Tyler 2000). The Sea Turtle Act was motivated by concern over worldwide declines in the populations of all seven species of sea turtles and by scientific studies that implicated shrimp nets in sea mortality.

One of the world's largest consumers of shrimp, the US also was one of the first nations to employ the ***turtle excluder device*** (TED). A TED is a grid trapdoor installed inside a trawling net that keeps shrimp in the net but directs other, larger objects or animals out (Figure 3.7). By the 1980s, TED technology had reached the point that, properly installed, 97% of sea turtles caught in shrimp nets could be released alive and unharmed without loss of shrimp (Joyner and Tyler 2000).

Earlier legislation had already required TEDs for all shrimp trawlers operating in the Gulf of Mexico and in the Atlantic Ocean off the southeast coast of the United States. The Sea Turtle Act went even further. It prohibited fish imports from any nation that failed to adopt sea turtle conservation measures comparable to those in the United States. Initially such sanctions were applied only to western Atlantic and Caribbean nations, which eventually complied. However, the largest shrimp importers to the US were Asian nations that did not use TEDs. As a result, the prohibitions of the Sea Turtle Act were largely symbolic and did little to protect turtles from shrimpers on a global scale.

As these events were taking place, the US was engaged in negotiations to ratify the General Agreement on Tariffs and Free Trade (GATT). The Clinton administration was reluctant to create controversy with Asian nations over sea turtles that could delay or halt ratification of GATT, and US officials delayed enforcement of the Act against its most important shrimp suppliers. Such reticence eventually led to a federal lawsuit by the Earth Island Institute, a US NGO. Earth Island Institute demanded that the provisions of the Sea Turtle Act be enforced uniformly against all nations exporting shrimp to the US. After a series of appeals, the Earth Island Institute won the case in the US Court of International Trade, forcing the US to ban imports from nations that had not complied with the Sea Turtle Act, including the largest Asian shrimp exporters.

The tuna and shrimp embargoes, now in full force, led to legal challenges by the sanctioned nations before the World Trade Organization (WTO). In separate but similar cases, the tuna and shrimp-exporting nations argued that the MMPA and Sea Turtle Act were violations of the free trade provisions guaranteed by GATT. In the case of tuna and dolphins, the European Community also joined in challenging the MMPA, because the embargoes prevented them from selling tuna they had purchased from Asian nations that did not comply with the MMPA to the US. The plaintiffs argued that, under the terms of GATT, an individual nation could not impose restrictions on imports from other nations, even for conservation reasons, that those nations had not been party to developing. Further, the US could not impose sanctions based on the *processing and production* of a product, but only on the product itself. That is, what mattered was the tuna in the can, not how the tuna got in the can (Salzman and Thompson 2003:220). In addition, the bottle-nosed dolphin (*Tursiops truncatus*), the main species affected by the tuna-fishing methods in question, was not an endangered species, and not subject to international protection. Finally, the plantiff nations charged that the entire embargo was only a ruse to protect US tuna fishers to give them an unfair competitive advantage in US markets, a form of protectionism wearing green clothing (Salzman and Thompson 2003:221).

The WTO ultimately agreed and ruled against the United States in the case of both dolphins and sea turtles, agreeing with the plaintiffs that the US laws constituted unfair barriers to free trade. The world conservation community condemned the GATT panel of the WTO for deliberately excluding environmental issues from consideration in its

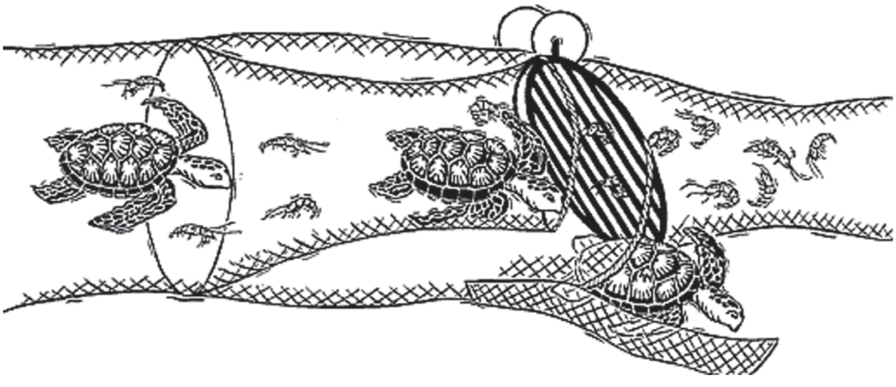

FIGURE 3.7. A Turtle Excluder Device (TED) that can be installed in a shrimp net to release sea turtles from the net. TEDs, properly installed, can reduce sea-turtle mortality associated with shrimp fishing by up to 97%. (Figure courtesy of US National Aeronautics and Space Administration.)

decision (Salzman and Thompson 2003:221). The US appealed the decisions, but its appeals were not successful (Joyner and Tyler 2000).

Although pledged to follow the rules of international law, the US continued its advocacy for the conservation of both marine mammals and sea turtles. In the former case, the US played a leading role in developing new international agreements, the La Jolla (California) agreement of 1992, a ten-nation agreement that established a voluntary program to limit dolphin mortality, and the Panama Declaration, which was signed by 12 nations in 1995. The Panama Declaration went beyond the La Jolla agreement in establishing a "permanent" mortality limit for dolphins and stricter enforcement systems. The purpose of the agreements was to foster better methods of harvesting tuna through a voluntary program of setting standards and procedures for dolphin protection. Their outcome was the establishment of the International Dolphin Conservation Program. To implement the La Jolla agreement, the US. Congress enacted the International Dolphin Conservation Act of 1992. To implement the terms of the Panama Declaration and nationalize the intent of the International Dolphin Conservation Program, Congress passed the International Dolphin Conservation Act of 1997 (Miller and Croston 1998).

The US maintained its commitment to sea turtle conservation by continuing to sponsor an already existing TED certification program for other nations. In addition, the US pledged to assist any government seeking help in developing a TED sea turtle protection program of its own (Joyner and Tyler 2000).

3.5.4. Outcomes and Future Prospects

These difficult cases involving tuna, dolphins, shrimp, and sea turtles offer insight into a world of complex interactions between national and international conservation law, public interest and private industry, and government bureaucracies and NGOs. They illustrate the fine line between conservation leadership and (in the eyes of some) conservation imperialism or economic protectionism disguised as conservation. Conservation laws of individual countries can no longer be enacted or enforced without first considering the interests of other nations or the likely international response. Although trade sanctions might be justified against processing and production methods, as well as products, of other countries that violate international conservation interests, an individual country cannot be confident that it will win in the international courts unless: (1) the measure is not unilaterally imposed and (2) the harm done is local (within the jurisdiction of the country imposing the sanctions) (Salzman and Thompson 2003:223). Today's worldwide commitment to global free trade has created international bodies, such as the WTO, whose decisions have the force of law. Such decisions may override the laws passed by a single nation in matters of international commerce, regardless of that nation's noble intentions for conservation. In the tuna-dolphin and shrimp-turtle decisions, the WTO displayed its own preference for multilateral and international agreements to reach conservation objectives as opposed to unilateral, national initiatives (Joyner and Tyler 2000); however, such decisions by the WTO appear to sacrifice conservation to commerce. The Dispute Settlement Body of the WTO rarely selects panel members and experts for their environmental expertise. Although the Dispute Settlement Body is authorized to seek expert advice on environmental issues, it rarely does so (Miller and Croston 1998). The perception that the WTO favors trade at the expense of conservation is part of the motive behind the anger and violence displayed toward the WTO by conservation and environmental organizations, among others, in the large public, and sometimes violent, demonstrations associated with the 1999 WTO meetings in Seattle, Washington and the 2000 WTO meetings in Washington, DC.

US laws like the MMPA and the Sea Turtle Act helped move the international community to higher standards on these conservation issues than would have been achieved without these initiatives. It is clear, however, in an increasingly global community that the US will have to improve its efforts to involve other nations in international conservation efforts, particularly conservation efforts that affect international trade, if it expects such efforts to be effective and permanent in their effects.

3.6. Synthesis

Environmental regulations and demands of conservation law press scientists to address and answer questions they may consider "unscientific." Likewise, law and policy require an integrated, interdisciplinary approach that conservation biologists may publicly endorse, but are privately unprepared to fulfill. Environmental problems on a worldwide scale may require a greater level of coordination than has historically been characteristic of the independent nature of science and scientists.

In the past, much of activity associated with conservation was focused on outcomes that were predictable effects of management actions. Goals such as sustained yield were based on an expectation of certain return. Today, conservationists are less concerned about certainty of return than about managing risk. Historically, environmental law has favored policies consistent with our past understanding of the rule of law (i.e., the consistent application of fixed rules that will yield a final, single decision that represents an absolute, moral ideal) (Tarlock 1994). As a result, individual environmental laws have been based on individual scientific premises, and have then continued the application of those premises regardless of what new studies uncovered. Today such legal certainties are inconsistent with the state of our knowledge of ecosystems. Conservation biologists' best estimates of genetic diversity, population persistence, and community ordination are also uncertain estimates. Modern conservation law and policy must mature to the point that they can deal with such uncertainty, rather than simply ignore or reject it, and therby better manage risk to threatened species.

The development of conservation law and policy demonstrates repeated themes. First, the scrutiny of a free press and the involvement of an educated populace enables private organizations and citizens to make a difference in how things turn out. Second, even failed attempts at international legislation, such as the Rio Summit, may produce positive results, and should be pursued toward the eventual goal of a comprehensive and coordinated system of international conservation legislation. Third, programs of lasting effectiveness in conservation are strongly affected by economic incentives, as evidenced by the efforts to save dolphins from tuna fishing and sea turtles from shrimp boats.

The future offers two challenges. Conservation biologists must become more astute in their understanding of law and policy to make their research effective in achieving conservation goals and they must become more sophisticated in learning how to change laws and policies, and formulate new ones, that will make conservation law more consistent with the scientific findings. Failure on the first front would make conservation biology an interesting but irrelevant discipline. Failure on the second would lead to irreconcilable conflicts between scientific and political communities, and the eventual disconnection of conservation science from conservation law.

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4

Biodiversity: Concept, Measurement, and Challenge

> *If there is danger in the human trajectory, it is not so much in the survival of our own species as in the fulfillment in the ultimate irony of organic evolution; that in the instant of achieving self-understanding through the mind of man, life has doomed its most beautiful creations.*
>
> E. O. Wilson 1992

In this chapter you will learn about:

1. **The concept of biodiversity**
2. **Methods of measuring and valuing biodiversity**
3. **Factors that affect levels of biodiversity and global patterns of species abundance**
4. **Preserving and managing biodiversity**

4.1. Biodiversity and Conservation Biology

Reflecting on conservation biology's beginnings, Michael Soulé realized that the major factor in conservation biology's emergence as a distinct discipline was the recognition among biologists of the accelerating and global loss of species – the "extinction crisis" (Soulé 1986). This shift in focus from the problem of "endangered species" to the problem of "loss of biodiversity" might sound like an exercise in biological semantics, but the change in emphasis is significant. Conservation biology's historical origins were in applied sciences such as forestry, wildlife management, fisheries, and range management (Chapter 1). Such disciplines, emerging as distinctive professional communities from the 1930s through the 1950s, were traditionally species-specific in their approach to management and their understanding of species' values. In this environment, studies of species' natural history and habitat requirements received priority. Resource management disciplines began to influence environmental law in the 1960s and 1970s, and the legislation drafted in this period reflected a similar emphasis. The US Endangered Species Act (Chapter 3), with its emphasis on individual species as the primary targets of conservation efforts, is the best, but not the only example of this type of legislation. Other conservation legislation, such as the Sea Turtle Act (Public Law 101–162) and the Marine Mammal Protection Act of 1972, displayed a similar focus.

The emergence of conservation biology reflected a shift in emphasis and a break with historic perceptions about the nature of the "endangered species problem." The traditional view of recent extinctions as a collection of tragic, individual case histories was replaced with a conviction that the global extinction crisis was caused by fundamental disruptions of ecosystem processes. Extinctions came to be perceived not as a sad parade of passing species, but as losses in genetics, community attributes, and ecosystem properties. With changes in perceptions of *what* was being lost came changes in perceptions of *why* species were being lost. New studies shifted emphasis from natural history to identifying the ecological processes that contributed to emerging patterns of extinction. The extinction crisis created an urgency to develop an alternative concept to that of "endangered species." That concept was *biodiversity*.

4.2. The Problem of Concept and Quantity: How Do We Know What Biodiversity is and How Do We Measure it?

4.2.1. A Conceptual Definition of Biodiversity

According to conservation biologist Stuart Pimm, the first use of the term ***biodiversity*** in scientific literature was by biologist Elliot Norse in a 1980 US government report (Pimm 2001). Norse was ahead of his time. As a term, the word "biodiversity" did not attain common use in science until after the American National Forum on Biodiversity in 1986 (Thompson and Starzomski 2006). In origin, biodiversity is a contraction of the term "biological diversity" (Wilson and Peter 1989). It has now been defined by a multitude of authors and agencies, but not always consistently (Table 4.1). To those engaged in the study of natural history, biodiversity represents the biotic elements of nature that can be described and classified. To environmental activists, biodiversity is an intrinsic value-laden quality of natural systems that should be preserved for its own sake. To conservation biologists, biodiversity is a measurable parameter relevant to an understanding of community structure, environmental processes, and ecosystem functions. Thus, before we attempt a definition of "biodiversity," we must recognize the "thought styles" and philosophical commitments that are entangled in the concept and affect the definition that we

TABLE 4.1. A diversity of definitions of biodiversity.

Source	Definition
Cox (1997)	The richness of the biosphere in genetically distinct organisms and the systems they represent.
Fielder and Jain (1992)	The full range of variety and variability within and among living organism, their associations, and habitat-oriented ecological complexes. Biodiversity encompasses ecosystem, species and landscape as well as intraspecific (genetic) levels of diversity.
Hunter (1996)	The diversity of life in all its forms and at all levels of organization.
Hurlbert (1971)	A function of the number of species present and the evenness with which the individuals are distributed among these species.
International Council for Bird Preservation (1992)	The total variety of life on earth. It includes all genes, species, and ecosystems and the ecological process of which they are part.
Johnson (1993)	The total diversity and variability of living things and of the systems of which they are a part. Biodiversity covers the total range of variation in and variability among systems and organisms at the bioregional, landscape, ecosystem, and habitat levels; at the various organismal levels down to species, populations, and individuals; and at the level of the population and genes.
Magurran (1988)	The variety and relative abundance of species.
McAllister (1991)	The genetic, taxonomic, and exosystem variety in living organisms of a given area, environment, ecosystem, or the whole planet.
Peet (1974)	The species richness or the number of species in the community, and the equitability or evenness with which importance is distributed among the species.
Reid and Miller (1989)	The variety of the world's organisms, including their genetic diversity and the assemblages they form. It is the blanket term for the natural biological wealth that undergirds human life and well-being. The breadth of the concept reflects the interrelatedness of genes, species, and ecosystems.
Sandlund et al. (1992)	The structural and functional variety of life forms at genetic, population, species, community, and ecosystem levels.
US Congress Office of Technology Assessment (1987)	The variety and variabiligy among living organisms and the ecological complexes in which they occur. Diversity can be defined as the number of different items and their relative frequency. For biological diversity, these items are organized at many levels, ranging from complete ecosystems to the chemical structures that are the molecular basis of heredity.
Wilson (1992)	The variety of organisms considered at all levels, from genetic variants belonging to the same species through arrays of species to arrays of genera, families, and still higher taxonomic levels; includes the variety of ecosystems, which comprise both the communities of organisms within particular habitats and the physical conditions under which they live.

Source: Table design by M. J. Bigelow.

choose (Mayer 2006). If we are not clear on these points, our ambiguity will grow into confusion about what is being conserved and why. To avoid the error, we begin by defining biodiversity as carefully as possible.

The 1992 Convention on Biological Diversity (CBD), the authoritative international treaty on biodiversity conservation, defines biodiversity as "…the variability among living organisms including, *inter alia* [among other things], terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are a part: this includes diversity within species, between species, and of ecosystems." This definition contains a large number of compromises and assumptions, but it does help to develop a normative concept of biodiversity that can be shared among many nations and thus build overall support for biodiversity conservation. The CBD itself reflects and reveals that biodiversity is a value laden term. In Article 1, the CBD states that the objective of the treaty is "the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources, including by appropriate transfer of relevant technologies, taking into account all rights over those resources and technologies, and by appropriate funding." Although written in prose that only an international diplomat could love, or easily understand, Article 1 clearly alludes to monetary and utilitarian benefits that people can gain, or hope to gain, from biodiversity. The same kind of value-laden understanding was present in the 2005 Mission Statement of the Society for Conservation Biology as *committed to developing the scientific and technical means for the protection*, *maintenance*, *and restoration of the Earth's biological diversity* (www.conbio.org 2005). Although "scientific and technical means" receive a central position in this statement, they are directed to the purpose of "protection, maintenance, and restoration" of biological diversity, not merely the study and classification of it. Biodiversity is here assumed to have an intrinsic value of its own that makes it worthy of receiving the attention of such scientific and technical means directed to the goal of its preservation.

Based on this kind of rhetoric at the highest international and scientific levels, we must acknowledge that biodiversity is protected because of its perceived value, not simply studied because it is interesting. Nevertheless, to practice conservation biology as a science, we need a definition that is more specific and more operational for analysis and inquiry. One of the best definitions of biodiversity is *the structural and functional variety of life forms at genetic, population, community, and ecosystem levels* (Sandlund et al. 1992). This definition is especially helpful because it focuses on the two ideas that make biodiversity a workable concept – that biodiversity is the entire array of biological variety, not simply a collection of individual species, and that the variety that defines biodiversity exists at multiple biological levels.

4.2.2. Biodiversity and the Definition of Species

If one were to ask, "what is a fundamental goal of conservation biology," a good answer would be "to save species." But, to be meaningful, such an answer requires a comprehensive understanding of what species are. The roots of the species concept extend beyond the history of science into the roots of philosophy itself. The idea of species was inherent and explicit in Plato's concept of the universe as an array of ideal forms. The actual thing observed, including all material objects, even living ones, was considered a shadow of its true form (*eidos*). Because each creature was a representation of a true or ideal form, variation among individuals within a population and among different populations was de-emphasized and emphasis was placed on the ideal that the creature imperfectly manifested. This formed the basis of the ***typological species concept*** that defined species as distinct morphological types.

The typological concept of species, subsequently combined with Aristotle's principles of logical divisions of organisms based on "common essence" (a unique attribute that makes the species what it is) was central to biology for many centuries, although modified with John Ray's concept that species "bred true" and with Linnaeus's concept that species were fixed, discrete, and natural entities created by God. With the advent and acceptance of the theory of evolution by natural selection, the view of species as discrete and immutable was replaced with Darwin's view of species as mutable and constantly changing. Darwin stressed the evolutionary integrity of species as being all individuals descended from a common ancestor, thus providing the foundations of the modern ***evolutionary species concept***. However, it can be difficult to determine the common ancestor of a species with certainty. Over 50 years ago biologist Ernst Mayr proposed a more practical criterion for sexually reproducing species. Mayr's definition of a species was "a group of actually or potentially interbreeding populations that are reproductively isolated from other such groups" (Mayr 1950). Today this definition, known as the ***biological species concept***, remains the most widely held use of the term among biologists. In Mayr's definition, the conceptual basis of the species definition is the criterion of reproductive isolation.

Problems inherent in the biological definition of species are many, and the precise demarcation of species remains challenging at best and impossible at worst. Part of the problem of dealing with the species concept is that biologists often focus on the definitional aspects of the word rather than on the information that is required to understand what species are and what causes species to exist. Species, as geneticist Jody Hey insightfully perceived "are the result of two processes: (1) the evolutionary processes that have caused biological diversity; and (2) the human mental apparatus that recognizes and gives names to patterns of recurrence" (Hey 2001:328). When conservation biologists talk about saving "species" as fundamental units of biodiversity, both they and their hearers must realize that they are trying to solve two related but different problems. These are trying to: (1) identifying the real evolutionary groups or units we are working with, and then determining how that will affect our conservation strategies for different groups and (2) devise and deploy conceptual categories that help us to speak about such groups to others (both scientists and the public) and to recognize their recurring patterns in all forms of biodiversity. If we keep the nature of the problems clear, we can also keep our focus properly fixed on the information we need to solve each kind of problem.

4.2.3. Contemporary Issues of the Species Concept

Today the species concept, as well as the science of taxonomy, has undergone and continues to experience a revolution in its definitions and concepts. Perhaps the most fundamental questions swirl around the foundational issues of taxonomy itself. The traditional methods of naming species are based on the system originally developed by the Swedish botanist, Carol Linn, who devised a system of ***binomial nomenclature*** which assigns a unique, two-word Latin name to every species, and thus permits scientists from any part of the world to have a common standard of nomenclature when speaking of individual species. The second word in the binomial is the creature's species name, which signifies that its traits are unique to its own kind, and the first word its genus name, a larger or "higher" taxonomic category in which it might be placed with other creatures like itself, yet different. Thus, the winter wren and the house wren are categorized as certain kinds of wrens by belonging to the same genus, *Troglodytes* (from the Latin, "one who lives in a hole," because some wrens are cavity nesters), but they are distinguished from one another as *Troglodytes troglodytes* (winter wren) and *Troglodytes aedon* (house wren). The charm of the binomial system is its combination of economy and uniqueness in providing a particular name to every designated species. Indeed, Linn liked the system so much he applied it to himself, Latinizing his own name to Carolus Linnaeus, the name by which he is better known today. Linnaean names are generally based on physical descriptions that summarize characteristics of the species described. For example, the fungus commonly known as the dark puffball, an unpleasant smelling mushroom that will release its spores in a visible cloud when pressed, goes by the Latin name of *Lycoperdon foetidum*, which can be roughly translated in English as "stinky wolf fart." But for all the color, and, sometimes, coarseness, of Linnean names, whose color and coarseness was meant to tell the biologist something about the characteristics of the organism, they provide no information about the phylogenetic relationships of organisms to one another.

Above the level of genus, Linnaeus, and those who used his system after him, developed general principles, and later elaborate rules, for organizing smaller groups, such as genera, into progressively larger groups, from family to order to class to phylum to kingdom. But, although modern groups are arranged according to hypothesized relationships of shared ancestry and common descent, the actual names of their different taxonomic categories do not convey information about such relationships.

The Linnean system depends heavily on typology. There is, for every group at every level, a "type" species, genus, and so on, that is considered most representative of the group and to which all other members of the group are compared. When new species are discovered, they are compared to "type species" for particular groups to assess how they should be named and placed in taxonomic hierarchies.

Intuitively, an alternative method of grouping organism would be to group them according to an assessment of evolutionary histories of features shared by all organisms in the group, that is, to more intentionally and foundationally group species as evolutionary units. For example, a ***cladistic approach*** would view a species group as a lineage of ancestral-descendent populations (clade). Different species would be distinguished from one another by the relative proportion of shared primitive and derived features (Figure 4.1). This kind approach to taxonomy has more recently given rise to an alternative paradigm in taxonomy, the so-called ***PhyloCode*** approach developed and advocated by taxonomists Kevin de Queiroz and Jacques Gauthier. In the PhyloCode system, a clade might be defined by the two most distantly related organisms in a group. Technically, these taxonomic extremists would be known as the "specifiers" and all organisms with the same last common ancestor as the specifiers would be placed within that group. Grouped in this way, names of organisms in the clade would not necessarily include any reference to families, order, classes, or even genera. And each name, for the species or the clade, would be based on the shared ancestry of its members (de Queiroz and Gauthier 1990). In PhyloCode, some genus names might be lost, some species names shortened or given a numeric designation, none of which generates enthusiasm among traditional taxonomists. Advocates of PhyloCode assert that, in fact, most traditional, Linnean names would survive the transition and usually end up covering the same array of organisms, to the extent that the older names actually reflect groups with shared phylogeny (Pennisi 2001). PhyloCode enthusiasts, of which there are a growing number, have been working steadily to develop a set of rules of nomenclature that will permit stability and consistency in naming, and that will also permit PhyloCode conventions to be used concurrently with preexisting nomenclature, all of which they have documented and continue to update on a PhyloCode website (www.ohio.edu/phylocode).

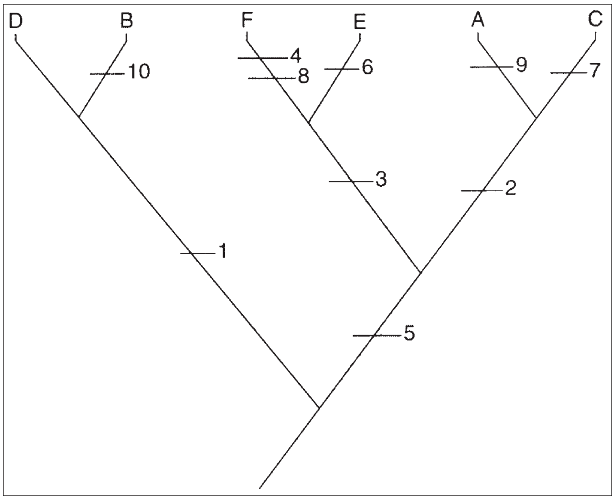

FIGURE 4.1. A *cladogram* is a tool that can be used to identify and conceptualize species as evolutionary units. This cladogram depicts relationships among species A–F based on 10 characteristics that occur in two discrete states (binary characters), one considered "primitive" (ancestral) and the other considered "derived" (advanced). The species are assumed to all be descendents of a common ancestor in which all traits were in primitive form. The point of change from the primitive to the derived condition for each character is used to determine the relationships of the species in the clade to one another, and is visually depicted by a horizontal bar and number. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications.* Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

4.2.4. Implications of the Species Concept in Conservation

The final resolution of the ongoing Linnaean – PhyloCode controversy is not yet in site, but the work of naming and categorizing the biodiversity of the Earth must continue.

In fact, the PhyloCode approach is symptomatic of an increasing emphasis in all areas of biology to increase the conformity between taxonomy and phylogeny. That is why, among the multiple species concepts extant today, it is the phylogenetic concept of species that, more than any other, has revolutionized the definition of species and our understanding of its reality. Modern techniques of molecular genetics now permit direct examination and comparison of nucleotide sequences and the organization of gene loci of individual organisms and populations. The modern ***phylogenetic species concept*** asserts that the way to define a species is through measuring genetic similarities, differences, and distances among populations or groups of populations. Although there remain obstacles to complete precision in measurement and definition, the phylogenetic approach is becoming the normative method for defining species. As a result, it has shifted the focus of conservation biology to give increased attention to genetic diversity as well as species diversity.

Although the phylogenetic species concept offers important gains in insight and precision for the work of conservation biology, it also raises significant problems when compared to the biological species concept. Paul-Michael Agapow of University College, London (UK) and his colleagues conducted a literature review of 89 published studies where a group of organisms was categorized under both phylogenetic and non-phylogenetic species concepts. Using non-phylogenetic species concepts, the studies covered 1245–1282 species, but under phylogenetic species assessment, the same studies identified 1912–2112 species, an increase of 49%. Across studies, average numbers in a species group increased an average of 121%. Studies of fungi showed a species increase of 300%, lichens 259%, plants 146%, and reptiles 137% (Agapow et al. 2004). The implications of these findings suggest that increasing use of the phylogenetic species concept will affect conservation efforts at multiple levels. First, because most procedures for identifying endangered species, such as those used by the IUCN's Red List or by the US Fish and Wildlife Service's Endangered Species List, consider both numbers of individuals in a population as well as geographic range and distribution, a phylogenetic species approach will effectively "split" more populations currently "lumped" under biological species and other approaches, such that more populations will fall below critical thresholds in both numbers and range size. For example, using IUCN criteria, Agapow et al. estimated that, regarding "Vulnerable" species, which have less than 1,000 indivduals, and "Endangered" species, with less than 250, a 49% increase in species number "…infers an average decrease in mature individuals per species of 32.8%. If we assume the number of mature individuals in "Vulnerable" species are distributed evenly throughout the band of possible values (250–1,000), a 32.8% drop will cause 10.9% of these species to have less than 250 individuals and so be reclassified as "Endangered."" (Agapow et al. 2004:169). Similarly, newly delineated phylogenetic species also are likely to have reduced ranges, and, on the basis of that criterion, the number of endangered species also may be expected to increase. In the United States, it has been estimated that the total budget needed for the Fish and Wildlife Service to achieve the recovery of all species would be around US$4.6 billion. As Agapow et al. note, "With widespread adoption of the PSC [phylogentic species concept], this already formidable amount could increase to US$7.6 billion, or the entire annual budget of the administering agency … for the next 120 years" (Agapow et al. 2004:169). And will an increasing estimate of the number of extant species, endangered or otherwise, create confusion, and eventually apathy, in the public mind? If these calculations are correct, has taxonomy become the enemy of conservation?

Our definition and understanding of what a species is affects how we will manage and conserve it. Conservation geneticist Martha Rojas framed the issue clearly by asking conservationists whether they are attempting to conserve species as types or species as evolutionary units (Rojas 1995). If we view species as types, argues Rojas, we will not consider the issue of maintaining their genetic variability. When we have protected an area containing the species of interest, we will consider our work complete. In contrast, if we view species as evolutionary units, then it is not merely a present population or individual that concerns us, but the evolutionary and speciation potential of the species itself. In this view, we must preserve, not only the organism, but also the organism's ability to respond to environmental change. We must preserve not only the population, but also the population's potential to give rise to a new species. We must protect not only the current biological entity and its contribution to biodiversity, but also the potential of the entity to enhance the sum of biodiversity in years to come.

The concept Rojas is addressing here has been formalized as the idea of the "evolutionarily significant unit" or ESU as the standard way of thinking about species in conservation. An ongoing problem with the ESU concept is the criterion for what is "significant" about the unit has never been unequivocally defined (Vogler and DeSalle 1994), and thus the selection of operational criteria to define ESUs often varies from case to case, with individual investigators using everything from bioregional distribution to morphological characters to molecular genetic markers, and a great many criteria in between (Ciofi et al. 1999). The concept of the ESU was intended to be based on some criterion for determining patterns of genetic variation within and between populations. In practice, it is often replaced with the more practical concept of the ***conservation management unit*** (MU) as a way of identifying a population or groups of populations that show evidence of genetic relatedness, but also are arranged spatially in such a way that they can benefit from a common management strategy. For example, Claudio Ciofi and his colleagues, using both molecular genetic markers and knowledge of geographic distribution of populations, were able to identify genetic-based MUs for conservation of the Komodo dragon (*Varanus komodoensis*) on the islands that form the bulk of its range in south-east Indonesia (Ciofi et al. 1999).

Attractive as the ESU concept is, much of the conceptual knowledge, mathematical measurement, legal protection, and ongoing management of biodiversity still make use of the biological concept of species. Although the biological concept has many faults, it has proven useful for sexually reproducing organisms because it possesses three important characteristics. (1) *It is a testable and operational definition*. The "test" is reproductive isolation; if individuals in the population breed with one another but not with individuals in other populations, the criteria for being a "species" has been met. (2) *The definition is compatible with legal concepts inherent in conservation laws*. Because species can be identified as independent entities, it is easier to assign protection, rights, values, and duties to species than to other levels of biodiversity. This is exactly what the US Endangered Species Act does. (3) Finally, *the definition focuses on a level of biodiversity that fits traditional expressions of conservation*.

Although the biological species concept possesses these and other tangible strengths, it is also ultimately flawed. The biological species concept has difficulty dealing with hybrids, and often fails to recognize populations with distinct lineages and adaptations if they happen to "look alike." Management practices designed to increase biodiversity typically aim to increase the number of species in a community, landscape, or ecosystem. Practices such as habitat manipulation, introduction of organisms, or controlling mortality through adjustment of hunting, fishing, or trapping regulations are species-specific in their applications and can be effective in altering biodiversity at many different levels. But all such management efforts assume that we have correctly identified the unit we are managing for, that we know what the "species" really is. If that identification is incorrect, our conservation efforts will be ineffective.

Conservation biologists increasingly recognize that their concept of species affects the way they approach conservation issues and the type of problems they attempt to solve. Our mental categories and historical knowledge of what a species is are imperfect, but whatever the limits of our understanding, we must get on with solving the problem of accurately measuring biodiversity if we would conserve it. And that is the critical question. How do we solve the problem of measuring the level of biodiversity present in communities, ecoregions, or even the entire world?

4.2.5. Measuring Biodiversity

4.2.5.1. What Biodiversity Measurements Tell Us

To be meaningful to science, various important features of biodiversity must be capable of measurement as mathematical variables and indices. Such indices must be understood for what they are, representations of *features of* biodiversity, not biodiversity itself. Nevertheless, conservation biologists must measure and express features of biodiversity in ways that are meaningful to others. Specifically, they must clarify what feature of biodiversity is being examined, what level of diversity is under investigation, and what dimension of that level is being evaluated. Let us begin at the level of species.

In practical and legal application, the most useful unit of biodiversity is most often that of species, which can be most easily understood by the public and clearly defined in the law. Other units of diversity, such as genetic, community, and ecosystem diversity, also exist, and are sometimes employed, depending on the conservation objective. Three levels of diversity – alpha, beta, and gamma – are recognized.

4.2.5.2. Alpha Diversity

Alpha diversity is the diversity of species within an ecological community, more practically, "the species richness of standard sample sites" (Vane-Wright et al. 1991), where "richness" is the number of species in the community. A broad definition of a community is "all populations of different species occupying a given area at a particular time." In practice, a single site is usually considered to have multiple community subsets distinguished from one another by common taxonomic levels or ecological traits. For example, a contiguous block of tallgrass prairie might be described in terms of its plant community, its invertebrate community, its small mammal community, and its bird community, to name a few. Specialized subdivisions may be used to identify functional relationships (for example, the predator community or the detritivore community) or more specialized traits. Alpha diversity in such a community is normally described as a measure of two attributes – species richness and species evenness. Table 4.2 provides an example of data from a community of birds in a tallgrass prairie that can be used to assess different dimensions of alpha (community) diversity.

A ***species list***, consisting of the total number and names of species recorded for a particular site, is a good first approximation of site-specific biodiversity. Species lists are often the only biodiversity indicator available from older, historical data, or from parts of the world where little systematic investigation has taken place. A refinement of the species list is a measure of ***species richness***. Unlike a species list, species richness is standardized to reflect the number of species recorded per sampling area or per some

TABLE 4.2. The density of avian species (singing males/10 ha) from two sites in tallgrass prairie habitats at the DeSoto National Wildlife Refuge, Iowa, USA, and the calculation of their comparative diversity.

Species	Site A	Site B
Common yellowthroat	8.24	1.21
Field sparrow	2.94	2.84
Dickcissel	1.18	2.23
Red-winged blackbird	0.29	0.81
Brown-headed cowbird	2.06	1.82
American goldfinch	1.47	1.02
Ringneck pheasant	0.59	1.63
Mourning dove	1.18	0.61
Eastern kingbird	–	1.60
Grasshopper sparrow	–	4.48
Northern bobwhite	–	2.64
Shannon diversity (H')	1.64	2.25

Source: Derived from data compiled by Van Dyke et al. 2004 and Van Dyke et al. 2007. Table design by M. J. Bigelow.

uniform number of observations. At the simplest level, consider an example from a bird community residing in a tallgrass prairie in Iowa (USA). In this example, Site A has 8 species and Site B has 11. If species richness is the sole measure of diversity, then the community with the larger number of species is considered more diverse.

As a measure of diversity, species richness has a number of positive attributes. The data needed are relatively easy to collect through samples or surveys. Individuals of different species need not be counted; the only data the observer needs to record is whether the species is present or absent. The final result is easy to present, interpret, and compare with other, similar communities, and the number of species present offers a useful first approximation of the biodiversity of the area or habitat.

Using species richness as an index of diversity has its drawbacks. Because species richness tells us nothing about the relative or absolute abundance of individual species in the community, we do not know whether the species present are equitable in numbers or distribution or whether the community is composed of a few abundant species and many rare ones. Note, for instance, in the data in Table 4.2, the two sites share many species, but have very different densities of these species. What is a reasonable and objective way to incorporate differences in abundance into our estimates of diversity?

In alpha diversity, a second dimension of community biodiversity is evenness. Our two sites, A and B, may have similar numbers and kinds of species; however, if site B not only has more species but its species are more equally abundant, while site A has fewer species and is dominated by just one species (common yellowthroat, *Geothlypis trichas*), then site B will be considered more diverse (Table 4.2). This determination has important implications for conservation. When a community is dominated by only one or a few species, it may be that the rarer species are at risk of disappearing from the site. The more common species might even be part of the problem if their behavior is detrimental to rarer species. Additionally, a distribution pattern in which one or a few species are far more abundant than all others may indicate that the habitat lacks a sufficient diversity of structure, patchiness, or resources to allow many species to exist together. An examination of species evenness can be a first step toward generating intelligent hypotheses about possible species interactions, and can lead to greater understanding of more complex processes that influence diversity in the community.

There are dozens of different measures of species evenness (Table 4.3). These measures are themselves only one group of metrics that are sometimes referred to as *biodiversity indices*. The most commonly used biodiversity indices generally make some measure of both species richness and species evenness, although other qualities of biodiversity can be evaluated. We will not review each metric individually, but it is helpful to understand how some of the more widely used measures of evenness make assessments of community diversity. One of these is the Shannon Index, which calculates diversity (H) as

$$H = -\Sigma_i\, p_i \ln(p_i),\ (\mathrm{i} = 1,2,3,\ldots\mathrm{S}),\ 0 \leq H' \leq \infty$$

where p_i is the proportion of the total community abundance represented by the ith species and ln (p_i) is the natural log of p_i. Numerous mathematical and statistical programs are available to calculate the Shannon Index and many other measures of evenness (e.g., Baev and Penev 1995). Any of these indices can be computed on a handheld calculator if the observer knows either the actual number of individuals of each species present or has some measure of each species' abundance or importance. What is important to note is that, in every case, diversity indices involving evenness incorporate quantitative measures of species abundance in relation to the total abundance of all species. Thus, the value of an evenness index increases as the number of species increases and as the species become more equal in abundance.

Individual, site-specific communities are not the only level at which biodiversity should be examined. Two other kinds of diversity, beta diversity and gamma diversity, also can be measured and evaluated.

4.2.5.3. Beta Diversity

Whereas alpha diversity measures the diversity of species *within* a community, ***beta diversity*** measures the diversity of species *among* communities. Thus, beta diversity provides a first approximation of area diversity or regional diversity. Beta diversity, sometimes called "beta richness," measures the rate of change in species composition in communities across a landscape. Ecologist R. H. Whittaker is credited with the origin of the term, and used it specifically

Table 4.3. Commonly used indices of alpha (community) species diversity and their associated formula.*

Index	Calculation	Descriptions, Distinctions, and Applications	Source
Brillouin's diversity index	$HB = \frac{\ln(N!) - \sum_i \ln(n_i!)}{N}$	The Brillouin index is recommended for fully censused communities and is therefore free from statistical error. However, its value changes when species numbers increase but proportions remain constant.	Pielou (1969, 1975)
Brillouin's evenness index	$HBe = HB / HB_{\max}$	Because this index is based on Brillouin's HB, it is not an estimate but an accurate statistic. Although more difficult to compute than most diversity indices, this index reduces the sensitivity of the estimate to changes in species density.	Pielou (1969, 1975)
Brillouin's maximum diversity index	$HB_{\max} = \frac{1}{N!} \ln \frac{N!}{\left[\left(\frac{N}{S}\right)\right]^{s-1} \left\{\left[\left(\frac{N}{S}\right)^{+1}\right]\right\}^{\gamma}}$	$HB_{\max}$ represents the maximum diversity possible with a given sample size and species richness. $HB_{\max}$ is used to calculate Brillouin's evenness index.	Pielou (1969, 1975)
Hill's diversity index	$N_1 = \exp\left[-\sum(p_i \ln p_i)\right]$	Hill's diversity index is an exponential form of the Shannon index. It is widely used, but is sensitive to single-species dominance.	Hill (1973)
Hill's reciprocal of C	$N_2 = \frac{1}{C} = (\sum_i p_i^2)^{-1}$	The reciprocal of the Simpson index (C) is commonly used along with Hill's N_1, but is not as dependent on the number of species as is N_1	Hill (1973)
Margalef's diversity index	$DMg = \frac{(S-1)}{\ln(N)}$	This widely used index is simple to calculate but best employed on large sample sizes.	Margalef (1968)
Pielou's index of evenness	$E = \frac{H'}{\ln S} = \frac{-\sum_i p_i \ln p_i}{\ln S}$	Pielou's evenness index (the ratio of observed diversity [H'] to the maximum possible diversity of a community with the same species richness [H'max]) is applicable to sample data, but mathematically relates evenness and richness, which are not necessarily related biologically.	Pielou (1969)
Probability of interspecific encounter	$PIE' = 1 - \sum_i p_i^2$	PIE′ is the complement of the Simpson index (1 − C), and estimates diversity instead of dominance.	Baev and Penev (1995)
Shannon index	$H' = -\sum(p_i \ln p_i)$	Probably the most widely used diversity index, the Shannon index is employed with both large and small sample sizes.	Shannon and Weaver (1949)
Simpson index	$C = \sum_i p_i^2$	The Simpson index is actually a measurement of dominance and assesses the probability that two randomly selected individuals from a community will belong to the same species.	Simpson (1949)

Source: Table design by M. J. Bigelow.

*S = number of species at site; N = total number of individuals; p_i = percentage of ith species at site; n_i = number of ith species at site.

to indicate the change in species composition of communities along a gradient (Whittaker 1975). The "gradient" is normally an environmental variable such as slope, moisture, or soil pH, which can be measured in the same way and at the same scale in all communities. The communities (sometimes designated with the more neutral term *biotic assemblages*) are measured along the gradient. Whittaker's mathematical measurement of beta diversity is

$$S/\alpha - 1$$

Where S is the number of species in the entire set of sites and α represents the average number of species per site, with sites standardized to a common size. In the simplest case, if every site has the same number of species, then $S/\alpha = 1$ and $S/\alpha - 1 = 0$ (i.e., the value of beta diversity is 0 when sites do not change in species composition, indicating a highly homogeneous landscape with respect to a particular environmental gradient). Such a result would indicate that the species examined had wide tolerances for that particular environmental variable, and thus had broad ecological tolerances and wide niche overlap. At the other extreme of beta diversity, suppose the entire collection of species was equal to 100, but the average number of species found at each site was only 10. Then $S/\alpha - 1 = (100/10)-1 = 10-1 = 9$. Theoretically, there is no upper limit to Whittaker's Measure of beta diversity, although in fact values above 10 are rare.

Beta diversity provides insights into three important but often neglected dimensions of biodiversity. First, *beta diversity gives a quantitative measure of the diversity of communities that experience changing environmental gradients*. As such, beta diversity provides a way of comparing different communities in a landscape in which important environmental variables change over distance. Second, *beta diversity provides insight into whether species in different communities are relatively sensitive or insensitive to changing environments, and whether associations of species are interdependent (individual species require the presence of other species in the assemblage to persist) or independent (species are added or lost in a more or less random fashion)*. Analyses of both trends are important in understanding biodiversity at the landscape level. Finally, *beta diversity can be used to measure non-environmental gradients, and thus measure how species are gained or lost relative to other factors*. For example, measures of beta diversity can be used, not only on different, adjacent sites, but on the same site at different times, thus determining whether the site increases or decreases in species over time. Such measurement is important in evaluating the effects of disturbance and time on a site's biodiversity, and can provide important insights into succession and its effects on community species composition.

Actual studies of beta diversity can provide insights into ecosystem biodiversity and composition that studies limited to alpha diversity cannot. For Example, Van Looy et al. (2006), examined the similarity of species pools of floodplain meadow plants between sections (technically, "reaches") of the River Meuse in western Europe. They determined beta diversity for every pairwise combination of reaches (i.e. from two reaches adjacent to one another to two reaches at opposite ends of the river) as equal to

$$\beta = \Sigma \text{ unique (unshared) species in each reach} / \Sigma \text{ all species in both reaches}$$

If each of two compared reaches has 100 unique species, and there only no species common to both reaches, then the value of β is

$$(100 + 100)/200 = 1.00.$$

In contrast, if each reach has only ten unique species, but the two reaches share 200 species in common, then the value of β would be

$$(10 + 10)/200 = 0.10.$$

Thus, the calculation of β provides an index of difference, or dissimilarity, with values ranging from 0 to 1, between reaches. The closer the value of β to 1, the more dissimilar the two reaches are. By computing this value for all pairwise combinations of reaches, Van Looy et al. were able to create a "dissimilarity matrix," (Table 4.4) and relate the occurrence of dissimilarity to geographical distances between reaches and to associated geographical, management, and hydroregime characteristics of the river. They found that increasing levels of beta diversity between reaches were not necessarily functions of the geographic distance between reaches, but mainly a product of differences in flow variability and surrounding valley form and soil characteristics, all of which were related to the maintenance of continuity and connectivity to the river's historic floodplain meadows. Overall, Van Looy et al. determined that invasive species were more prevalent in floodplain meadows associated with the more disturbed and "disordered" reaches of the rivers, while native, often more specialized species of plants predominated in floodplain meadows associated with less disturbance (Van Looy et al. 2006).

TABLE 4.4. Dissimilarity values (Σ unshared species in each reach/Σ all species in both reaches) for floodplain meadow plants between different reaches (sections) of the River Meuse in western Europe.

	I	II	III	IV	V	VI
I						
II	0.497					
III	0.56	0.24				
IV	0.52	0.42	0.32			
V	0.52	0.5	0.45	0.31		
VI	0.45	0.54	0.52	0.39	0.34	

Source: Van Looy et al. Order and disorder in the river continuum: the contribution of continuity and connectivity to floodplain meadow biodiversity. *Journal of Biogeography*. Copyright 2006 by Blackwell Publishing.

4.2.5.4. Gamma Diversity

Gamma diversity refers to the diversity of species across larger landscape levels. In measurable terms, gamma diversity is the product of the alpha diversity of a landscape's communities and degree of beta differentiation among them (Vane-Wright et al. 1991). Thus, the term *gamma diversity* is used to denote the diversity of different kinds of communities within a landscape. Conceptually it is "the rate at which additional species are encountered as geographical replacements within a habitat type in different localities" or "a species turnover rate with distance between sites of similar habitat, or with expanding geographic areas" (Cody 1986). Unlike beta diversity, gamma diversity is independent of habitat and is calculated as

$$dS/dD[(g + l)/2],$$

the rate of change of species composition with respect to distance. D is the distance over which species turnover occurs. g and l are respective rates of species gain and loss.

The three types of diversity can change independently of one another (Figure 4.2), but in real ecosystems, they are often correlated. High levels of diversity, whether alpha, beta, or gamma, almost always lead to some form of natural rarity (Cody 1986). As species are added to a community, numbers of individuals in individual species typically decline, a phenomenon that has been called ***alpha rarity***. ***Beta rarity*** occurs in ***habitat specialists***; they are abundant in one environment, but rare or absent from environments which manifest even slight changes in one or more critical

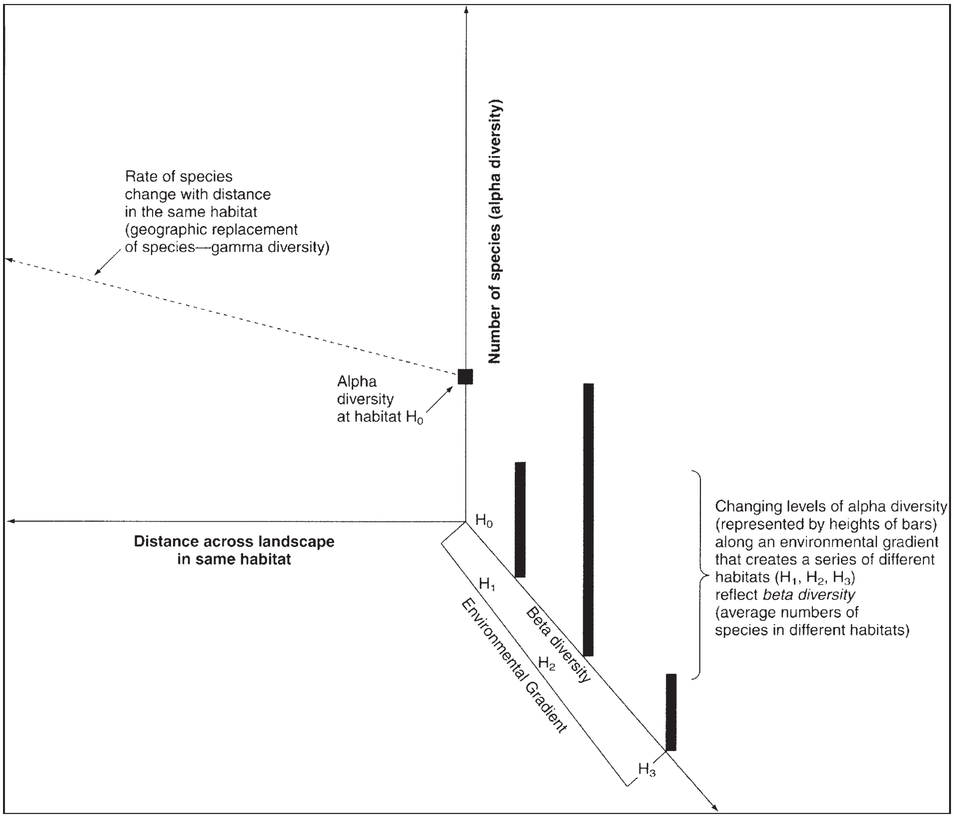

FIGURE 4.2. The relationships among alpha, beta, and gamma diversity at a landscape scale. (Modified from Cody 1986. Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

variables. ***Gamma rarity*** describes species that may have large populations in local communities and demonstrate broad environmental tolerances, but are restricted to particular geographic areas and so are lost with increasing distance from their population centers. All of these dimensions of biodiversity must be measured and understood before a biologist can interpret the state of a system's biodiversity and the processes that produce it.

4.2.6. Application and Integration of Diversity Measures to Address Issues in Conservation: A Case Study from Eastern Amazonia

The ability to measure biodiversity with precision allows conservation biologists to monitor changes in biodiversity that are concurrent with human activities in the landscape. With this application in mind, Lopes and Ferrari investigated the relationship between biodiversity and human activity in the tropical rainforests of eastern Amazonia in Brazil (Lopes and Ferrari 2000). They measured three dimensions of alpha species diversity that have been previously described mathematically in Table 4.3: species richness (Margalef's index), species diversity (Shannon's index), and species evenness (Pielou's index); and related each to two elements of human disturbance: forest fragmentation and hunting pressure (Table 4.5). Every measure of species diversity declined as disturbance became more intense. More specifically, species diversity declined with increasing hunting pressure and increasing forest fragmentation and species evenness decreased with increasing forest fragmentation (Table 4.6). This study demonstrated that precise use of varying measures of biodiversity can be helpful in determining which kinds of disturbance affect which dimensions of diversity in a given community.

4.2.7. Problems of Diversity Indices and Alternative Measures

Although all mathematical measures of diversity provide precise and quantifiable indices of species richness, evenness, or dominance, they possess inherent problems that can obscure rather than enlighten conservation efforts. Controversies about the concept of diversity became intense in the early 1970s, with some mathematical ecologists going so far as to call species diversity a "nonconcept" because of its semantic, conceptual, and technical problems, and to claim that "diversity per se does not exist" (Hurlbert

TABLE 4.5. Species diversity indices recorded in 200 km transect samples at five study sites in eastern Amazonia, Brazil. CRAI = Companhia Real Agro-Industrial, Tailândia, Pará. FBA = Fazenda Badajós, Ipixuna, Pará. FSM = Fazenda São Marcos, Irituia, Pará. GBR = Gurupi Biological Reserve, Maranhão. FMV = Fazenda Monte Verde, Peixe-Boi, Pará.

	Site				
Variable	Fazenda Monte Verde, Peixe-boi,	Fazenda Badajós, Ipixuna, Pará	Fazenda São Marcos, Irituia, Pará	Companhia Real Agro-industrial, Tailândia, Pará	Gurupi Biological Reserve, Maranhão
Area (ha)	200	8,000	10,000	17,485	341,000
Forest disturbance rank	5	4	3	1	2
Hunting pressure rank	4	3	2	5	1
Mammal species	9	9	13	8	15
Total number of individuals	610	281	346	186	343
Shannon's index of diversity (H')	0.984	1.615	1.797	1.697	2.160
Pielou's index of evenness (E)	0.448	0.735	0.701	0.816	0.798
Margalef's index of richness ($R1$)	1.247	1.419	2.053	1.34	2.389

Source: Data from Lopes and Ferrari 2000. Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.

TABLE 4.6. Trends in species richness, species diversity, and species evenness in response to hunting pressure and forest fragmentation in eastern Amazonia, Brazil.

	Disturbance Effect	
Variable	Forest Disturbance	Hunting Pressure
Sightings of nongame species	Increase	No effect
Sightings of game species	No effect	Decrease
Species diversity (H')	Decrease	Decrease
Species evenness (E)	Decrease	No effect

Source: Data from Lopes and Ferrari 2000. Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.

1971). Semantics problems arise when species richness and species evenness are conflated. Richness and evenness, although often correlated, can exhibit inverse relationships along some gradients. (i.e., increases in species evenness can be accompanied by decreases in species richness). Mathematical measures can create problems because they do not always correspond to ecological importance in quantifying diversity, so the value of each species in a diversity index is not the same as the value of the species in ecosystem function or conservation priority. Different diversity measures may yield different values for the same community or change the rank order of diversity in different communities (Hurlbert 1971). Species richness and evenness also tend to be influenced by the number of samples taken and the size of the area sampled. Finally, some values of alpha diversity, such as the Shannon Index, can give nearly identical values for very different patterns of species abundance under some conditions (Huston 1994).

Although the mathematical and conceptual problems of measuring and interpreting diversity indices have been resolved or, in some cases, selectively ignored, some problems associated with diversity measurement are persistent. For example, species richness and evenness often increase as a result of human activities that lower the conservation value of the overall landscape. Habitat fragmentation tends to increase the amount of edge (lengths of habitat borders), and edges are often associated with greater species richness and alpha diversity. However, the sorts of species attracted to edges typically are ***habitat generalists*** with large dispersal distances and wide geographic ranges. Habitat specialists, often "interior species," tend to disappear as large, contiguous blocks of habitat are fragmented and edge increases. Thus, even as diversity is increasing, species of greatest rarity and highest conservation value might be disappearing. This problem illustrates why conservation biologists must be well informed about the species composition of a community, and not use diversity indices alone to evaluate the community's ecological health or conservation value.

Conservation biologists are increasingly concerned about the fact that mathematical diversity indices treat all species as taxonomically equivalent even though this is not appropriate for setting conservation priorities. One species of panda might not be the conservation equivalent of one species of rat, even if both are equally abundant in a given community. One solution to this problem is to employ some form of a ***phylogenetic diversity index*** (PDI), which incorporates known information about the evolutionary history and phylogeny of a taxonomic group, and thereby permits a way of estimating the taxonomic uniqueness or distinctiveness of each individual unit, such as species. Vane-Wright et al. (1991) propose one form of PDI as a "taxic diversity measure" that measures diversity not as species richness or species evenness but as the amount of "taxonomic distinctness" present in a community, based on the number and abundance of different taxonomic levels present (Figure 4.3). Measures of taxonomic diversity also can be used in combination with other data, such as endemicity indices, to conduct "critical faunal analysis" (Ackery and Vane-Wright 1984), in which fauna of different sites are ranked according to the number of endemic species present. The site with the highest number of endemics is ranked first, the lowest last. Then the minimum number of sites is selected that will preserve all endemic taxa (i.e., a complete list of "critical areas") (Vane-Wright et al. 1991). Combined with knowledge of taxonomic diversity, such an index permits species or other taxonomic groups to be scored according to both taxonomic uniqueness and endemicity, giving highest ranks, and highest conservation value, to groups that are both geographically and phylogenetically unique.

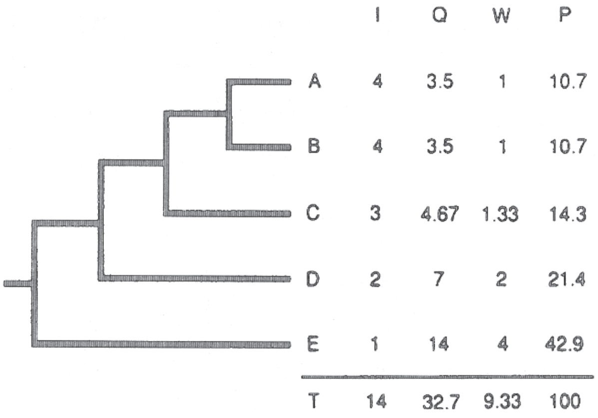

FIGURE 4.3. The derivation of an index of taxonomic distinctness, or weight, using five terminal taxa, A–E. Column I indicates the number of groups to which each terminal taxon belongs within the system, a basic measure of taxonomic information. For example, Taxon A belongs to four groups and so receives a score of 4, but Taxon E belongs to only one group, and so receives a score of 1. Values in Column *Q* represents the total taxonomic information (ΣI, in this case, 14) divided by the taxonomic information of each taxon (I_j) or $\Sigma I/I_j$, or a "basic taxic weight," or measure of taxonomic uniqueness. Values in Column *W* provide the *standardized weight* for each terminal taxon by dividing the *Q* value for each taxon (Q_j) by the lowest Q value (Q_{min}, in this case, 3.5). Values in Column *P* provide the percentage contribution for each terminal taxon to total diversity ($Qj/\Sigma Q$). Column totals provide aggregate scores for each index, *I*, *Q*, *W*, and *P*. (Reprinted from Biological Conservation 55, Vane-Wright et al. 1991. Copyright 1991, with permission of Elsevier.)

4.3. The Problem of Process and Pattern: What Explains Variation in Local Biodiversity?

4.3.1. Niche Assembly Theories of Biodiversity

A well-established, "traditional" group of general theories of biodiversity invoke ***niche assembly theories*** of communities. Niche assembly theories assert, in various ways and at various temporal and spatial scales, that different species are able to live together in communities only if they differ sufficiently in niche separation, that is, in the way they use resources. This view rests on the principle of competitive exclusion, formally stated as ***Gause's Law of Competitive Exclusion***. The name comes from experiments performed by the biologist G. F. Gause during the 1930s. Gause mixed different species of *Paramecium*, an aquatic, ciliated protozoan often used as a model organism in biological studies because of its small size, rapid reproductive rates, and minimal maintenance needs, in order to understand how similar species could coexist in the same environment. Gause determined that *Paramecium* species that fed on the same food in the same way (for example, at the same depth in the water column) could not coexist. One species invariably displayed a slight competitive advantage, expressed in more rapid reproduction or more efficient feeding strategies, that doomed its less able competitor to extinction. Only combinations of species in which each used the resource in a slightly different way, avoiding direct competition, were able to live together.

Gause's results, eventually formalized as a biological principle, have produced and continue to stimulate much research in studies of community ecology, particularly in research on competitive relationships. The implication of Gause's perspective in ecology is that communities are eventually organized by competitive interactions. In his classic paper," Diversity and the coevolution of competitors, or the ghost of competition past," the ecologist J. H. Connell proposed that present diversity, as well as ecological organization, in a community is primarily a product of past competitive interactions (Connell 1980). Thus, the expectation is that biodiversity will increase as a function of competition for resources. Areas with more opportunity for specialization in obtaining resources (i.e. areas with a greater variety of kinds of resources, not just more resources) will permit greater niche specialization, and ultimately possess greater biodiversity.

In this traditional view, the two primary components of biological diversity in any community are the number of ***functional types*** and the number of ***functional analogs*** (Huston 1994; Figure 4.4). Among animals, functional types are sometimes referred to as "guilds" and among plants as "life forms." Recall that, in human societies,

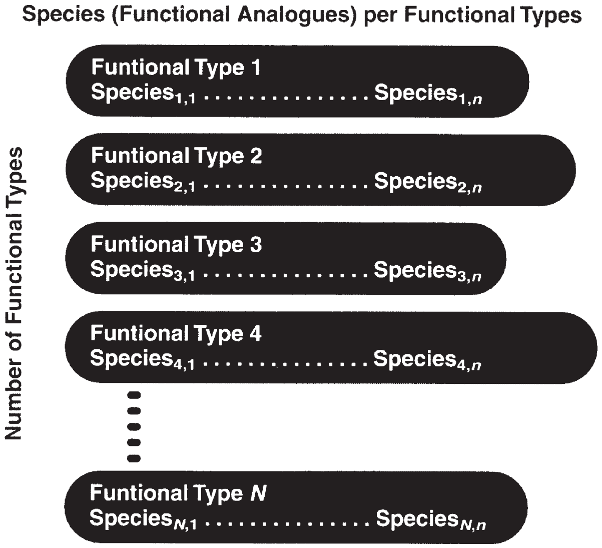

FIGURE 4.4. Two components of species diversity: functional types (ovals) and functional analogs (species within ovals). Diversity increases as the number of functional types and/or functional analogs increase. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

guilds were associations of workers of similar skills. In an ecological community, guilds, or functional types, are species that exploit similar resources, often using similar behavior "skills" to acquire them. In a community of birds, for example, we might have nectar feeders, fruit eaters, seed eaters, insectivores, omnivores, birds that specialize in killing other birds or mammals, and whatever other resources the community may provide. Niche assembly theories predict that processes causing an increase in the number of functional groups (increased number of available niches) yield an increase in species diversity.

In a niche-assembly perspective, species are not equivalent ecologically. It is precisely their differences which drive niche separation. Direct competition (trying to get the same resource in the same way at the same time) will be avoided because even small differences in efficiencies between competitors will lead to the extinction of the less efficient competitor. Thus, as a result of such past competitive contests and their resulting elimination of similar species, current communities are composed of ecologically distinct members who have evolved to avoid direct competition for resources.

Niche assembly theory sees communities as "limited membership" associations, as well as highly interactive and mutually interdependent. The way to predict community composition is through an understanding of ecological niches and the interactions that apply to them. Community stability is derived from the adaptive equilibrium of each member species, the best competitor in its own niche.

Niche assembly theory explains, or is at least consistent with, many observed characteristics of communities, such as resource partitioning among similar species. One of the classic examples of such partitioning can be seen in foraging strategies observed in birds feeding in the same tree. Ecologist Robert MacArthur demonstrated this with one group of birds, North American wood warblers (subfamily Parulidae). With elegant mathematical and conceptual models in one of science's most classic studies, MacArthur was able to demonstrate that, although multiple species of warblers in one tree were all obtaining food by gleaning invertebrates from the tree's foliage, they did so at different heights and on different parts of the tree and used different hunting and foraging strategies to do it, thus avoiding any direct competition (MacArthur 1958). Similarly, community ecologist Martin Cody was able to demonstrate that communities of Mediterranean grassland birds were organized primarily by the degree of ecological differences (niche specialization) among species. Even as individual species changed over large landscape scales, niche use remained relatively constant, such that certain ecological "roles" were predictably filled in the same way even among communities with entirely different species compositions (Cody 1986).

Niche assembly theory also has a personal appeal to many in the scientific community. If communities are based on niche separation, there is value in understanding the role of every species. Thus, natural history retains a prominent place in conservation. Niche assembly theory also provides a basis for ethics of ecocentrism, such as the Leopold land ethic, which imparts value to individual species in a community because of their functional roles in maintaining the community and its functions over time. For these and other reasons, there is strong professional and personal attachment to a niche assembly perspective of community composition, but there are alternative perspectives.

4.3.2. The Unified Neutral Theory of Biodiversity

In contrast to niche assembly theories, which stress competition as the driving force of community organization, Stephen P. Hubbell, a professor of plant biology at the University of Georgia, has proposed an alternative theory of biodiversity known as the ***unified neutral theory of biodiversity and biogeography*** (Hubbell 2001). In contrast to traditional niche assembly theories, Hubbell believes that communities can be best understood as open, non-equilibrium assemblages of species that are only weakly competitive or co-adapted, if at all. In Hubbell's own words, communities are "thrown together by chance, history, and random dispersal" (Hubbell 2001:8). Species' presence, absence, and relative abundance are dictated by random speciation, dispersal, ecological drift (a form of demographic stochasticity, the random variations in a population's rates of birth and death), and extinction.

Hubbell's theory is called "neutral," because processes that affect demographic variables in every species in a trophic group, such as rates of birth, death, migration and speciation, affect every individual with the same proportional weight. Thus, neutral, to Hubbell, means "per capita ecological equivalence of all individuals of all species in a trophically defined community" (Hubbell 2001:6). No selection pressure affects the per capita probabilities of birth, death, migration, and speciation. Community species abundance bears no footprint of past events. Hubbell calls the theory "unified" because the same mathematical parameters can be used to predict the diversity of many types of communities, and because it unites theories that explain the level of diversity in a given community with the spatial relationships of community distribution, such as the species–area relationship documented in biogeography studies. Let us work out this example.

One of the earliest patterns observed in the study of biodiversity has been the direct relation between species richness and area, a relationship first observed by early biogeographers comparing the number of species on islands of different sizes (Figure 4.5) (Darlington 1957:483). The ***species–area relationship*** provided a foundational concept for the development of the theory of island biogeography. Island biogeography's most basic and familiar equation, $S = cA^z$, states that the number of species (S) on an island is a constant power of the island's area (A), mediated by two constants, c and z. c is a constant specific to a particular taxonomic group. Mathematically, z is the slope of the species–area relationship. Conceptually, that makes z the "extinction coefficient" that integrates the rate of extinction in the group to the number of species associated with the area. The species–area relationship has important conservation implications. For example, a typical species–area relationship implies that a 90% reduction in available habitat will result in a loss of 50% of the species that live exclusively in that habitat, and a 75% loss if 99% of the habitat is lost. Although never a perfect predictor in any specific setting, variation in the area associated with different sites usually can explain more than 50% of the variation in species richness among the sites (Gaston and Spicer 2004:51).

Like the island biogeography theory, Hubbell begins by mathematically defining assumptions about the relationship between area and species. Specifically, that

$$J = \rho A$$

where J is the number of individuals in the defined area or taxon, A is the area, and ρ is the density of individual organisms per area. At this point, the equation is hardly profound. It simply means, for example, that if we have an area with 50 trees per ha and the size of the area is 100 ha, then the area A will contain 5,000 trees (J). What is interesting is that, when sampling an area of homogeneous habitat, the relationship is very precise (Figure 4.6) and is well documented in many kinds of organisms in different landscapes and habitats, even when the species in the examined group (in this case, trees) changes radically from place to place. This precise relationship suggests the possibility that the dynamics of ecological communities may be a zero-sum game, in which there is a limited amount of occupiable space, regardless of niche. This prospect led Hubbell to a fundamental theorem about biodiversity: *large landscapes*

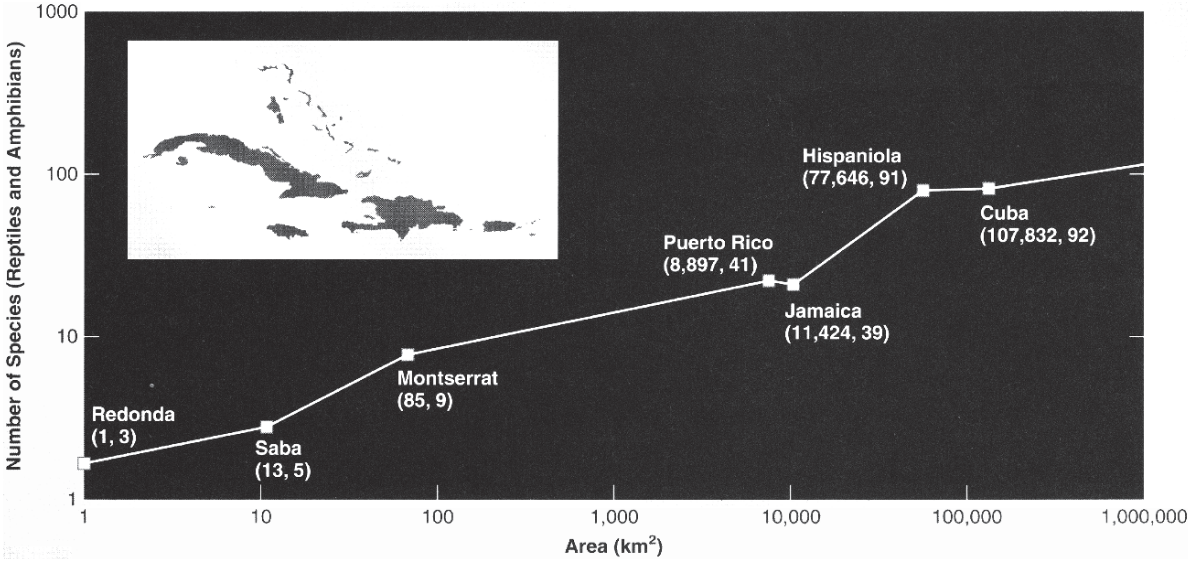

FIGURE 4.5. A general species–area relationship among some Caribbean islands. Note that species richness on islands increases with increasing area of the island. (Derived from data from Darlington 1957. Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

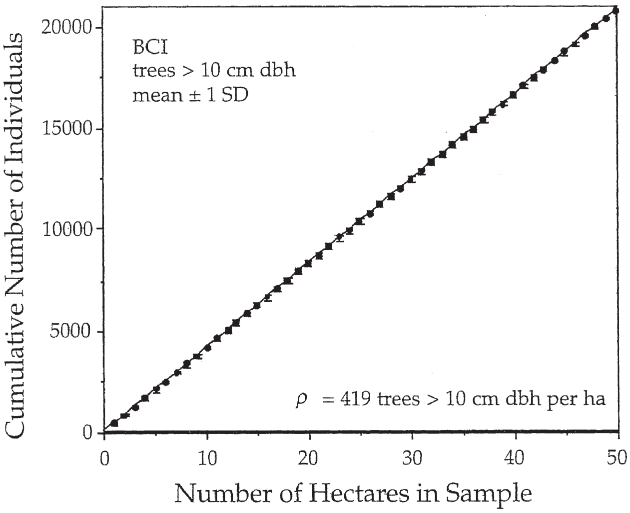

FIGURE 4.6. The individuals–area curve for a 50 ha plot of tropical moist forest on Barro Colorado Island, Panama for trees with trunk diameter > 10 cm. The curve shown represents the mean of 100 random starting points for accumulation of area within the plot. (Hubbell, Stephen P., The Unified Neutral Theory of Biodiversity and Biogeography. Copyright 2001 by Princeton University Press. Reprinted by permission of Princeton University Press.)

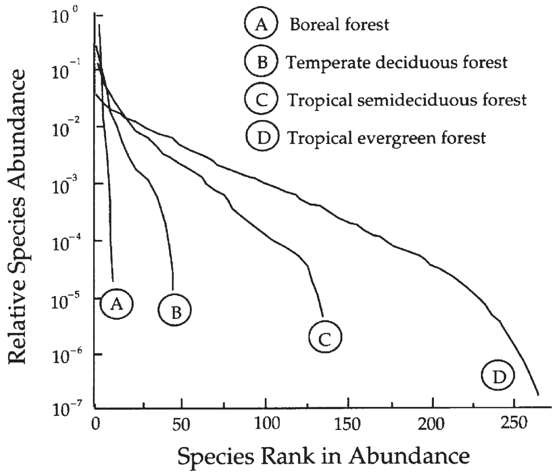

FIGURE 4.7. Dominance-diversity curves for tree species in four kinds of closed-canopy forest spanning a large latitudinal gradient. Ecologist and author of the unified theory of biodiversity Stephen P. Hubbell notes that "the four curves seem to represent a single family of mathematical functions, suggesting that a simple theory with few parameters might capture the essential metacommunity patterns of relative species abundance in closed-canopy forests." (Hubbell, Stephen P., The Unified Neutral Theory of Biodiversity and Biogeography. Copyright 2001 by Princeton University Press. Reprinted by permission of Princeton University Press.)

are almost always biologically saturated with individuals of a specified metacommunity or taxon (Hubbell 2001:53).

Upon examining the relationship between relative species abundance and species ranks in abundance, the so-called ***dominance-diversity curve***, of tree communities in four different kinds of forests (Figure 4.7), Hubbell noted, "what is especially intriguing about these dominance-diversity curves is not their differences, but their similarities. The four curves appear to form a family of closely related functions.... As species richness decreases, the distribution of relative species abundance becomes steeper, and the common species become even more dominant" (Hubbell 2001:117–118).

Based on these and other data, and the mathematical implications of his assumptions, Hubbell asserts that the diversity of a community can be described by a dimensionless biodiversity parameter, θ, a community's "fundamental biodiversity number," which determines the diversity pattern or species–abundance distribution and the species–area relationship of the metacommunity at large spatial scales. θ controls "not only the equilibrium species richness but also the equilibrium relative species abundance in the metacommunity. Parameter θ is a dimensionless, fundamental quality that appears pervasively … at all spatio-temporal scales" (Hubbell 2001:124).

To better understand what θ actually is, consider its extreme cases. If every individual sampled represents a new and different species, θ = ∞, and the dominance–diversity distribution would become a horizontal line (Figure 4.8).

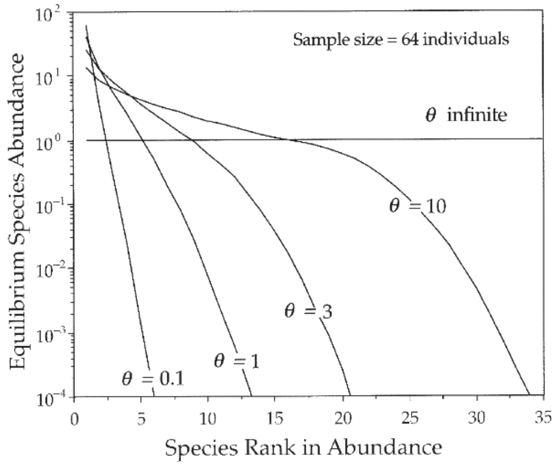

FIGURE 4.8. Expected metacommunity dominance-diversity distributions for a sample of 64 individuals at various values of the biodiversity parameter θ. When θ is small, such as where θ = 0.1, the expected dominance-diversity curve has a steep slope and the community has high dominance by a few species. When θ becomes larger, the dominance-diversity relationship begins to exhibit an S-shaped curve typical of many species-rich communities. When θ becomes infinite, the distribution approaches a horizontal line, reflecting that every individual in the sample is a new and different species. (Hubbell, Stephen P., The Unified Neutral Theory of Biodiversity and Biogeography. Copyright 2001 by Princeton University Press. Reprinted by permission of Princeton University Press.)

On the other hand, if the distribution of a community collapses to a single monodominant species, $\theta = 0$. θ is then best understood as a measure of diversity relating a species relative abundance to its rank in total abundance. It can be derived from the formula

$$\theta = 2\rho A_M \nu$$

where ρ is, as previously, is the mean density of individuals per unit area in the metacommunity, A_M is the area of the metacommunity, and ν is the speciation rate.

Thus, the unified theory predicts the existence of a dimensionless biodiversity number, θ, which is equal to twice the speciation rate times the metacommunity size. If you know or can estimate the speciation rate and the local community size, you could predict species richness and relative abundance in that community.

Hubbell's theoretical efforts have drawn attention for several reasons. First, the unified neutral theory has been able to provide predictions which closely match observed data (Figure 4.9). Second, the theory explains the traditional species area curve as being derived from fundamental processes of population dynamics, something which traditional niche assembly theories have had difficulty doing. Third, Hubbell's theory explains several things about the species–area curve, including its variation in slope, as a result of its dynamic dependence on varying rates of speciation, dispersal, and extinction. Hubbell and others readily admit many instances in which the neutral theory does *not* fit observed patterns of species abundance. Additional modeling also reveals weaknesses. For example, Zhou and Zhang experimented with Hubbell's theory by incorporating small Allee effects into the model, such that small populations suffered accelerated declines in reproductive rates. When Allee effects were incorporated into the neutral model, there were significant declines in species richness, radically different dominance diversity curves, and declines in times of species coexistence in the community (Zhou and Zhang 2006). However, Hubbell's theory is likely to be persistent in biological investigations, including investigations in conservation biology, because it generates specific and testable predictions about community composition that can be evaluated by theoretical modeling and experimental analysis.

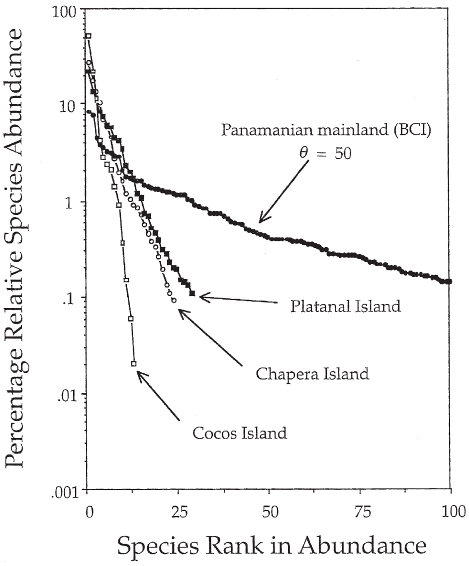

FIGURE 4.9. Dominance-diversity distributions for forest communities on Chapera, Cocos, and Platanal Islands of the Pearl Archipelago in the South Atlantic compared to the dominance-diversity distribution of the forest community of Barro Colorado Island, Panama, assumed to be representative of Panamanian mainland forests. Note the correspondence of observed dominance-diversity distributions in these communities to those predicted by the Unified Neutral Theory of Biodiversity (Figure 4.8). (Hubbell, Stephen P., The Unified Neutral Theory of Biodiversity and Biogeography. Copyright 2001 by Princeton University Press. Reprinted by permission of Princeton University Press.)

4.4. The Problem of Dispersion: Where is Biodiversity Located?

4.4.1. Global Patterns of Biodiversity

Diversity is a complex phenomenon. Just as diversity cannot be explained by a single hypothesis or theory or measured with a single statistic, it cannot be easily described on a global scale. Each major taxonomic group (not to mention most minor ones) shows important and unique patterns in the distribution of its diversity. We will identify some patterns shared by more than one taxon, as well as some exceptions.

All major classes of vertebrates, as well as plants, show marked increases in the number of species as one moves from temperate to tropical latitudes (Figure 4.10) (Reid and Miller 1989; Huston 1994). However, there are exceptions in which diversity increases in temperate, or even polar areas instead of decreasing. These include sea birds, lichens, marine benthic organisms, parasitic wasps, and soil nematodes (Huston 1994).

As with latitude, diversity tends to show an inverse relationship to altitude, particularly in plants. This is not surprising given that increases in altitude produce environmental and climate effects similar to those of latitude. In plants, diversity tends to be highest at low to middle latitudes and lowest at high latitudes and altitudes.

Within these broad patterns, important regional and habitat trends in diversity exist. In marine environments,

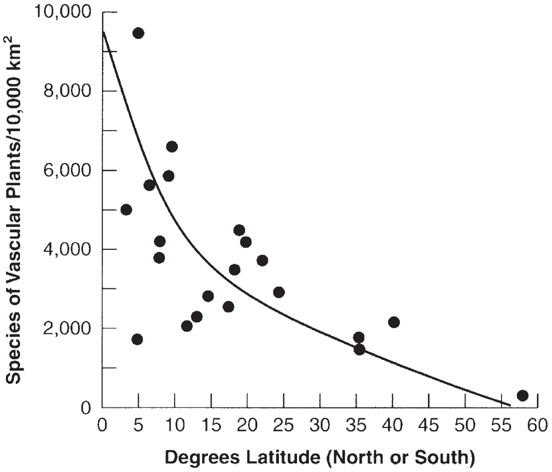

FIGURE 4.10. Latitudinal patterns in species richness from tropical to temperate regions. In most taxa the number of species increases from temperate to tropical regions. (Based on data from Reid and Miller 1989. Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

diversity is highest in coral reef habitats, in coastal zones and estuaries, and is higher in tropical marine ecosystems than in temperate ones. In terrestrial habitats, the diversity of tropical rainforests is higher than all other habitats; it is, in fact, legendary. Investigators have found up to 300 different tree species per hectare in study plots in Peru (Wilson and Peter 1989). As many ant species (43) and genera (26) were collected from an individual tropical rainforest *tree* in Peru as are present in all of the British Isles (Wilson 1989). In temperate areas, freshwater wetlands contain disproportionately high levels of species diversity at the landscape level. Wetlands may be particularly important in systems of low diversity. For example, boreal swamp forests contribute high biological diversity to otherwise low-diversity boreal forest ecosystems (Hornberg et al. 1998). Island floras and faunas tend to have high rates of endemism, and make disproportionately high contributions to world biodiversity.

4.4.2. Biodiversity Indices: Can We Find "Hotspots" with Incomplete Information?

There is not enough money, labor, and expertise to identify, count, and map the distribution of every species at a global scale in time frames that can assist current conservation decisions. Thus, conservation biologists have been engaged for some time in attempting to find noncensus indicator methods that can rapidly and reliably identify areas with disproportionately high levels of biodiversity. The earliest efforts to accomplish this goal relied on the ***umbrella species*** concept for biodiversity preservation. The umbrella species approach assumes that if an area containing a species or group of species of conservation interest, for example, large mammals, is preserved, this protection will benefit species in other taxa, thus protecting a high level of biodiversity. Unfortunately, empirical data have provided little support for this assumption. Instead, most data indicate that taxonomic distributions of organisms are remarkably independent. No one group predicts the distributions of other groups (Prendergast et al. 1993).

Recent studies of biodiversity have attempted to gain a more comprehensive picture of regional biodiversity by combining knowledge of ranges of traditional "species" with information on phylogenetic lineages based on genetic analysis. For example, Leslie Rissler and her colleagues compared spatial patterns of endemism and conservation value of 22 species of reptiles and amphibians in California (USA) with the 75 phylogenetic lineages they contained, as determined from previously published genetic studies (Rissler et al. 2006). The phylogenetic analysis revealed several areas of high conservation value and unsuspected areas of phylogenetic endemism that would not have been identified in a species level analysis (Figure 4.11). Such analysis also aided in the detection of sites that could be described as "phylogenetically irreplaceable." Traditionally, managers have designated irreplaceable sites as those protected to ensure the persistence of a species. Using a phylogenetic approach, irreplaceable sites also would include those sites that must be protected to ensure the persistence of unique genetic lineages. As Rissler et al. noted, "…our results confirm that many geographic regions harbor cryptic evolutionary diversity, and an understanding of conservation value will differ if species rather than lineages are used in conservation assessments … to conserve evolutionary history, it is essential to understand phylogenetic patterns within species because species are poor surrogates for lineages" (Rissler et al. 2006:660, 664).

As we have already learned from the work of Agapow et al. (2004), phylogenetic approaches, while discovering valuable and otherwise hidden lineages of high conservation value, also tend to increase estimated numbers of endemic, vulnerable, and endangered species that must be protected, thus often straining already limited resources for conservation. Even at the level of primary investigation, there may be insufficient information available to conduct the kind of multiple-level, complementary species and lineage assessments of biodiversity that characterized the efforts of Rissler et al. The problem before us is intimidating. Is there any way to index global biodiversity without species' censuses and exhaustive phylogenetic analyses?

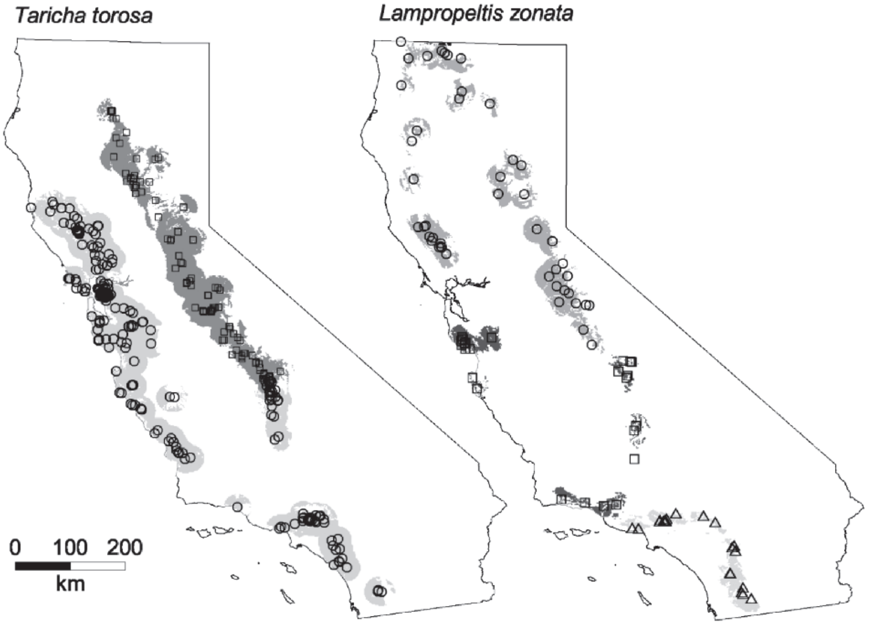

FIGURE 4.11. Examples of the differences between species distributions (shaded areas) and lineage distributions (unique symbols) of one species of amphibian, the California newt (*Taricha torosa*), and one species of reptile, the California king-snake (*Lampropeltis zonata*). Note that, in each species, phylogenetic analyses reveal distributions of unique evolutionary lineages that would have been overlooked in an analysis of species' distribution alone. (Rissler et al. 2006. Copyright 2006 by The University of Chicago.)

4.5. The Problem of Quantity: How Much Biodiversity is There?

4.5.1. General Considerations

Until the recent crisis of extinction and biodiversity loss, the question, "How many species are there?" was seldom considered important enough to ask, much less answer. Today fewer than 2 million kinds of organisms have been recognized as "species," but the total worldwide estimate is much higher, and much less precise. Scientists estimate that there are anywhere from 5 million to more than 50 million species (May 1988; Erwin 1997). That range is, to say the least, a very wide confidence interval. Why are we so uncertain about such a vital aspect of conservation biology?

The first difficulty is that we have explored the world very unevenly. About two-thirds of all species classified have come from temperate areas, especially from North America and western Europe, where high human population densities, accessibility of most areas, and detailed scientific exploration all have contributed to a relatively high level of knowledge of local species. Insects contribute the greatest numbers to the worldwide total of identified species, and most of these are from temperate regions. However, in larger terrestrial vertebrates which have been especially well studied all over the world, there are roughly twice as many tropical species as temperate ones. If the same ratio holds for insects, this would mean that there are about two unclassified species of tropical insects for every classified temperate insect species. If this is true, the total estimate of species worldwide would be revised upward to —3–5 million (May 1988). But we find, as we increase the precision of our estimates of biodiversity, that we are increasingly confronted with more and more cases of managing rarity.

4.5.2. Biodiversity and Rarity

4.5.2.1. The Problem of Rarity

As Darwin remarked over 150 years ago, "Rarity precedes extinction" (Darwin 1859). That insight remains true today. Thus, rarity is an essential concern in the study of conservation biology, and an important dimension of biodiversity. Diversity and rarity are positively correlated in communities and environments. Alpha, beta, and gamma diversity will increase from community to landscape to region if the number of species and their proportional evenness of abundance increase. Therefore, the densities of most species will become lower as diversity becomes higher at all scales. If conservationists desire to maximize biological diversity, they must learn to manage rarity.

The archetypal rare species is one characterized by small populations, specialized habitat requirements, and a restricted geographic range. Some species actually do meet all three of these criteria. For example, the endangered Kirtland's warbler (*Dendroica kirtlandii*) has an estimated world population of fewer than 2,000 individuals, breeds only in homogeneous, young, even-aged stands of jack pine (*Pinus banksiana*), and concentrates approximately 60% of its breeding effort in three counties in the state of Michigan in the United States. But rarity is not always so well defined.

A first step to understanding factors underlying rarity is offered by Rabinowitz et al. (1986). Their typology was

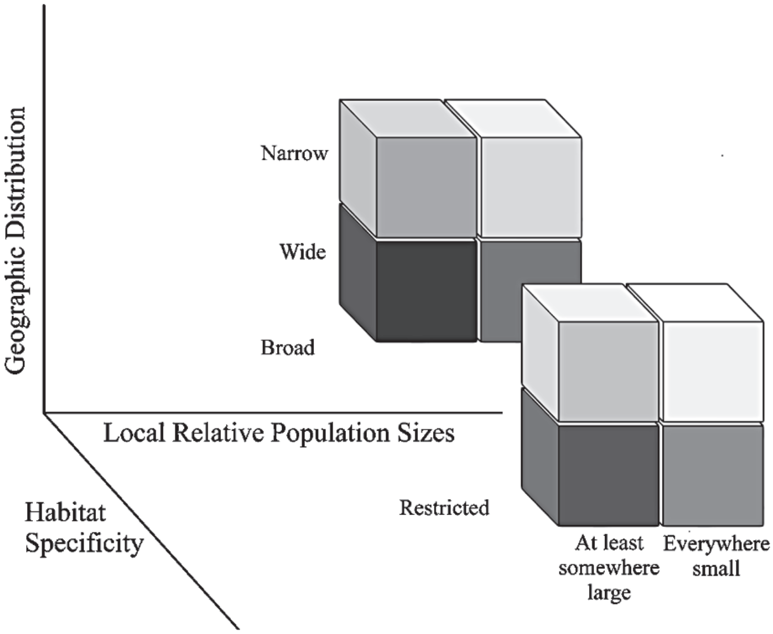

FIGURE 4.12. Eight categories of species abundance in British wildflowers based on geographic range, habitat use, and relative population size. Note that only one category (broad habitat specificity, wide geographic distribution, and large local population) can truly be considered "common." Species in all seven other categories are rare in one or more dimensions. (Original figure design by M. J. Bigelow.)

Color	Geographic Distribution, Habitat Specificity, Local Population Size	Example
■	wide, broad, at least somewhere large	*Deschampsia cespitosa*, tufted hair-grass
■	wide, restricted, at least somewhere large	*Hypochoens maculata*, spotted gosmore
■	wide, broad, everywhere small	*Ammophila arenaria*, marram grass
■	wide, restricted, everywhere small	*Draba muralis*, wall whitlow grass
▨	narrow, broad, at least somewhere large	*Primula scotica*, Scottish birds-eye primrose
▨	narrow, restricted, at least somewhere large	*Agrostis setacea*, bristle-leaved bent grass
□	narrow, broad, everywhere small	(no example)
□	narrow, restricted, everywhere small	*Lloydia serotina*, alpine lily

based on eight categories created by three dichotomies: (1) Is the population dense or sparse? (2) Does the species use many different habitats or only one or a few habitats? (3) Does the species have a wide geographic distribution or a narrow geographic distribution (Figure 4.12)? Rabinowitz et al. (1986) surveyed botanical experts on 177 species of wildflowers in the United Kingdom where abundance and distribution data were available and attempted to place each species in one of the eight categories. Seventeen species were controversial regarding their abundance, but the other 160 produced consensus. Of these, only about a third (36%) were "common" in all categories, having large populations, wide distributions, and broad range of habitats. Only 2% were floral equivalents of the Kirtland's warbler, with small populations, specialized habitat preferences, and restricted geographic ranges. The majority of species (62%), were "rare" in at least one dimension of their pattern of abundance. Each dimension of rarity needs attention to better understand its effect on overall biodiversity.

4.5.2.2. Habitat Generalists Versus Habitat Specialists

Habitat generalists are species that can exploit a variety of habitats in a given geographic range. Within that range, they are relatively invulnerable to extinction through habitat loss or general changes in land use because, if one habitat is changed or destroyed, they move to another or adapt to the altered habitat. For example, the Sulawesi Tonkean macaque (*Macaca tonkeana*), an Indonesia species of monkey that traditionally dwells in minimally disturbed tropical forests, has shown ability to thrive in forests that are heavily altered and converted to agricultural plantations for the production of coffee and cacao. The macaques accomplish this adaptation by changing their food habits, activity patterns, and group size in the altered habitat (Riley 2007). In contrast, habitat specialists are highly successful and competitive in one or a few types of habitat, but unable to use others. For example, several species of dragonflies (Order Odonata) found in the Cape Floristic Region of South Africa use only a small subset of the vegetation communities endemic to this region, including three species on the IUCN Red List (Grant and Samways 2007). For habitat specialists like these dragonflies, loss of preferred habitat at local or regional levels is catastrophic and leads directly to endangered status.

4.5.2.3. Large Populations Versus Small Populations

Some species almost always occur in large numbers and high densities. Their abundance may be the result of natural history traits such as high reproductive rates, high

FIGURE 4.13. The mountain lion (*Puma concolor*), an example of a "rare" species with extensive geographic range and wide habitat tolerance but uniformly low population density. The mountain lion historically had the widest distribution of any American mammal other than *Homo sapiens*, but local densities were almost always less than 1 individual /20 km^2. (Photo courtesy of US Bureau of Reclamation.)

FIGURE 4.14. The Haleakala silversword (*Argyroxiphium sandwicense*), an example of a "rare" species with a dense population of individuals (50,000) confined to a single site, the crater of Haleakala, a Hawaiian volcano. (Photo courtesy of Forest Starr and Kim Starr.)

rates of juvenile and adult survival, or strong competitive abilities that allow them to dominate other species. Other species, even if widespread geographically, are never abundant anywhere. Natural history traits that contribute to low abundance include low reproductive and survival rates, specialized diets (especially among carnivores), and the need for large areas to find food or complete their life cycles (a particular problem for large-bodied, territorial animals). The mountain lion (*Puma concolor*) (Figure 4.13) historically possessed the largest distribution of any American mammal (Jones et al. 1983), ranging from the southern tip of the Arctic circle in North America to southern Chile and Argentina in South America, and from the Atlantic to the Pacific in both hemispheres. As a large, territorial carnivore, one resident lion requires a minimum of 16–20 km^{2}., and some use areas of up to 600 km^2 (Hempker 1982). As a result, no single area ever had large numbers of mountain lions. When naturally small populations become isolated, prey availability is reduced, and habitat is restricted. As in the case of the subspecies known as the Florida panther (*Puma concolor coryi*), the population can become imperiled and the probability of extinction increases.

4.5.2.4. *Widespread Distribution Versus Restricted Distribution*

If a species possesses a widespread distribution, like the mountain lion, the probability of persistence at regional or global levels can remain high although individual populations are threatened, or even exterminated, in particular areas. If such species have dispersal abilities sufficient to allow individuals to move among populations, they comprise a metapopulation that can periodically re-colonize sites suffering local extinction (Chapter 8). If a species has a more restricted distribution, it is more susceptible to changes associated with local or regional land use, human population growth, or climate change. An extreme example of a restricted distribution is the Haleakala silversword (*Argyroxiphium sandwicense*) (Figure 4.14), a striking plant covered with fine, silvery hair and producing a tall flower stalk at maturity, after which the plant dies. Fifty thousand individuals live on the Hawaiian island of Maui, but all in a single location, the crater of the volcano Haleakala.

4.5.3. The Problem of Endemism

4.5.3.1. *Endemism in the Extreme – A Case History*

The silversword, in its extremely restricted geographic range, illustrates a pattern typical of other restricted species. This is the phenomenon of ***endemism***, in which a species is restricted to a particular area or region. Many tropical species are highly endemic, although there are examples of endemic temperate and polar species as well. The restricted range of an endemic species makes it especially vulnerable to extinction because local changes in land-use patterns or climate affect all individuals. If a species is concentrated in a single area, there is no "reserve" of individuals in another area that might be used to replenish the species if it suffers extinction. Because endemic species are at such high risk, some conservation biologists have argued that the problem of extinction should be studied and understood primarily as the problem of endemism, and endemic species should receive priority in protection (Pimm 1998). Endemism also has attracted attention among conservation biologists because it is natural to form the hypothesis that endemism and biodiversity should be correlates. It has been assumed that if we protect regions with high levels of endemism we are also protecting areas with high levels of biodiversity. But is this assumption true?

4.5.3.2. Endemism, Biodiversity, and Rarity

Studies by John Lamoreux and his colleagues have suggested that endemism and richness in four terrestrial vertebrate classes (mammals, birds, reptiles and amphibians) are, when considered separately and by ecoregions, highly correlated between and among classes. For example, variation in species richness in mammals explained nearly two-thirds of the variation in richness in the three other vertebrate classes. Similarly, variation in endemism in birds explained over 61% of the variation in endemism in other vertebrate classes (Table 4.7) (Lamoreux et al. 2006). However, correlations between endemism and richness were low, with one variable explaining less than 10% of the variation in the other in any vertebrate class, as well as in all classes combined (Table 4.7). Although correlation between endemism and richness is low at global scales, aggregate regions selected for high levels of endemism captured more species than expected by chance alone. A selection of only 10% of the Earth's terrestrial surface area captures 56.5% of terrestrial vertebrate endemic species and 61.6% of all vertebrate species (Lamoreux et al. 2006).

Although the findings of Lamoreux et al. offer encouragement to conservation biologists who have long hoped, and often assumed, that different taxonomic groups have congruent geographical patterns of diversity, the priority targets of conservation efforts are not *all species* but *endangered and threatened species*. If the correlations identified by Lamoreux et al. also apply to threatened and endangered species, this would mean that protecting threatened species in one group would protect threatened species in other groups. In a more focused analysis on rare and endangered species of high conservation priority, Richard Grenyer and his colleagues found that, although there was correlation in species richness patterns among birds, mammals, and amphibians, congruence in the distribution of rare and threatened species in these groups was markedly lower, especially for the very rarest species. Using high resolution databases with grid cells that could be adjusted to varying spatial scales, Grenyer et al. found, for example, that, if amphibians were treated as the conservation target, 55.5% of amphibian species would be present in a complementary set of grid cells selected to contain all members of a surrogate group, such as birds. But the same relationship dropped to only 22.5% for rare (endemic) species of amphibians and birds, and 31% for threatened species (Table 4.8) (Grenyer et al. 2006). Noting Lamoreux et al.'s study specifically, Grenyer et al. attributed past findings of high correlations of richness in different taxonomic groups as a function of scale, specifically that the ecoregions used by Lamoreux et al. were too big to detect meaningful patterns of correlation, or the lack of it. "The average size of those ecoregions," argued Grenyer et al., "(5.5×10^4 km^2) … is much larger than our grid cells and is several thousand times larger than

Table 4.7. Pearson correlation coefficients of terrestrial vertebrate diversity measures. For richness and endemism, values reflect the correlation of that variable in the given class with a counterpart index of richness or endemism in the three other classes. Values for richness × endemism indicate the correlation between endemism and richness within a class and of the four classes combined.

	Amphibians	Reptiles	Birds	Mammals	Four Classes
Richness[a]	0.591**	0.380**	0.715**	0.668**	
Endemism[b]	0.503**	0.587**	0.612**	0.490**	
Richness × Endemism[c]	0.096**	0.085**	–0.068	–0.099	–0.025

Note: *$P < 0.05$; **$P < 0.01$

[a] Correlation between class richness and a richness index of the three remaining classes

[b] Correlation between class endemism and an endemism index of the three remaining classes

[c] Correlation between richness and endemism within each class, and of the four classes combined

Source: Reprinted from Nature 440, Lamoreux et al. 2006. Copyright 2005, with permission from Nature Publishing Group.

TABLE 4.8. Patterns of cross-taxon surrogacy across birds, mammals, and amphibians. Values represent the percentage of species in the target group represented in complementary sets of grid cells designed to contain all members of the surrogate group (mean ± standard deviation). N_{spp} is the total number of species in the surrogate group. N_{cells} is the number of cells in the optimal complementarity set.

Richness Index	Surrogate Groups	$N_{spp.}$	N_{cells}	Target Groups (% Of Species Represented In Set)		
				Birds	Mammals	Amphibians
Total	Birds	9,626	421	–	79.4 ± 0.3	55.5 ± 0.7
	Mammals	4,104	509	91.7 ± 0.1	–	61.1 ± 0.5
	Amphibians	5,619	831	90.9 ± 0.2	86.2 ± 0.2	–
	Birds, mammals	13,730	714	–	–	68.4 ± 0.5
	Birds, amphibians	15,245	1,028	–	89.8 ± 0.2	–
	Mammals, amphibians	9,723	1,077	95.0 ± 0.1	–	–
	All three groups	19,349	1,223	–	–	–
Rarity	Birds	2,424	380	–	43.3 ± 1.1	22.5 ± 1.3
	Mammals	1,026	432	68.3 ± 0.4	–	27.0 ± 0.7
	Amphibians	1,405	560	63.7 ± 0.5	51.6 ± 0.6	–
	Birds, mammals	3,450	656	–	–	35.7 ± 0.9
	Birds, amphibians	3,829	808	–	63.1 ± 0.6	–
	Mammals, amphibians	2,431	858	77.9 ± 0.2	–	–
	All three groups	4,855	1,033	–	–	–
Threatened	Birds	1,096	282	–	51.7 ± 0.9	31.2 ± 1.4
	Mammals	1,033	357	60.7 ± 0.6	–	39.7 ± 0.9
	Amphibians	1,856	454	62.7 ± 0.4	59.7 ± 0.4	–
	Birds, mammals	2,129	518	–	–	49.2 ± 0.6
	Birds, amphibians	2,952	627	–	67.2 ± 0.5	–
	Mammals, amphibians	2,889	690	72.4 ± 0.4	–	–
	All three groups	3,985	821	–	–	–

Source: Reprinted from Nature 444, Grenyer et al. 2006. Copyright 2006, with permission from Nature Publishing Group.

most protected areas. … Our results show that congruence among rare and threatened species declines rapidly as the scale approaches that more relevant to real protected areas. High congruence at the ecoregion scale does not, therefore, mean that reserves in ecoregions will also show high congruence" (Grenyer et al. 2006:94).

In the very rarest species (those with the smallest 10% of ranges), pairwise correlations between groups were negative. This means, as Grenyer et al. put it, "…the very rarest birds, mammals, and amphibians live in different places from one another" (Grenyer et al. 2006:94). Thus, Grenyer et al. concluded "…even among terrestrial vertebrates, the extent to which rare and threatened species from one group can act as a surrogate for corresponding species in other groups is severely limited, especially at the finer scales most relevant to conservation." Therefore, "… designing effective protected area networks will require high-resolution data on the distribution of multiple taxa and an understanding of how these relate to ecosystems" (Grenyer et al. 2006:95).

In some areas, endemism is characteristic of nearly all species. For example, 90% of Hawaiian plants and 100% of Hawaiian land birds are endemic. In the Fynbos region of southern Africa, known for its unusual and unique plant communities, 70% of all plant species are endemic. On a continental scale, 74% of Australian mammals are found only in Australia (Pimm et al. 1995). Many conservation organizations have made endemism the controlling criterion in prioritizing areas for protection. This focus is the basis of the ***hotspot*** concept for ranking areas for conservation, one form of a ***geographic-based approach*** to conservation that will receive more attention in our later examination of habitat and landscape conservation (Chapter 10). Today the conservation community recognizes 34 biodiversity hotspots (Figure 4.15). In each, the number of endemic species is high. Even higher is the ratio of endemics to the area in which they occur. These areas, covering only 1.4% of the Earth's terrestrial surface, contain 44% of the world's known terrestrial plant species and 35% of known terrestrial vertebrates (Malcolm et al. 2006).

Unfortunately, the geographic endemism characteristic of the world's hotspots is not consistent in different taxonomic categories (van Jaarsveld et al. 1998). This fact makes it hard to apply hotspot criteria uniformly. Areas with high rates of endemism for birds might not have many endemic amphibians (Pimm 1998). Areas rich in species diversity might be poor in genus or family diversity, and vice versa. Therefore, the prospect of finding "indicator taxa" that could be used as indices of diversity of other taxonomic categories is not promising (van Jaarsveld et al. 1998). The diversity of different taxa cannot often be protected

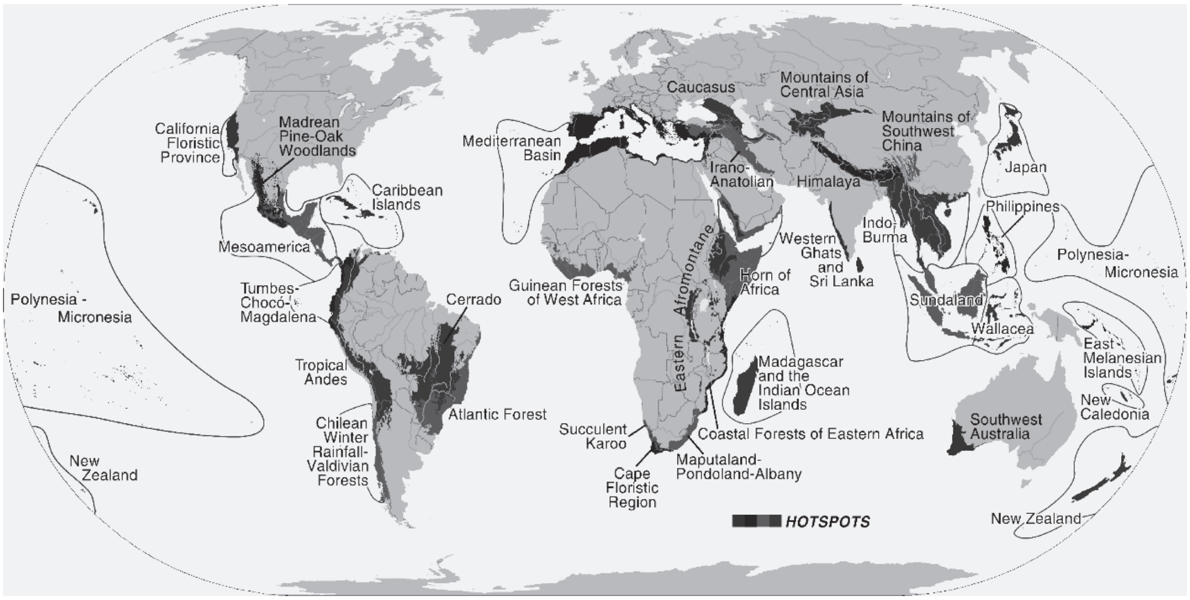

FIGURE 4.15. The world's 34 officially recognized "hotspots" of biodiversity as identified by Conservation International. Covering only 1.4% of the world's land area, hotspots are estimated to contain 44% of all terrestrial plant species and 35% of all terrestrial vertebrate species. (Figure courtesy of Conservation International website www.conservation.org and the Biodiversity Hotspots website www.biodiversityhotspots.org. Reproduced with the kind permission of Conservation International.)

in the same conservation areas. Conservation strategies to protect endemic species must be comprehensive, both biologically and geographically, to be successful, and must contain specific information about the distribution of individual species, not just indicator taxa or community diversity (van Jaarsveld et al. 1998).

TABLE 4.9. Species richness and endemism among higher plants on selected islands.

Island or Archipelago	Total Species	Endemics	% Endemic
Borneo	20,000–25,000	6,000–7,500	30
New Guinea	15,000–20,000	10,500–16,000	70–80
Madagascar	8,000–10,000	5,000–8,000	68.4
Cuba	6,514	3,229	49.6
Japan	5,372	2,000	37.2
Jamaica	3,308	906	27.4
New Caledonia	3,094	2,480	80.2
New Zealand	2,371	1,942	81.9
Seychelles	1,640	250	15.2
Fiji	1,628	812	49.9
Mauritius, including Reunion	878	329	37.5
Cook Islands	284	3	1.1
St. Helena	74	59	79.7

Source: Compiled by Whittaker 1998 using data from Groombridge 1992 and Davis et al. 1995. Note that 10 of the 13 selected islands have flora that are composed of 30% of more endemic species. Table design by M. J. Bigelow.

4.5.3.3. Endemism and Island Species

Many island species represent cases of endemism that merit conservation priority. By their very nature, island species usually meet at least two of the three requirements for rarity. First, island species have highly restricted ranges. They are typically endemic to their islands, unless they can fly, swim, or float for long distances. Not surprisingly, the high rates of species endemism on islands are associated with high rates of biodiversity per unit area (Table 4.9; Whittaker 1998).

The high endemism and per area biodiversity of island flora and fauna are often coupled with extreme vulnerability to extinction. Many island species specialize in the use of habitats unique to their own island or island system and may occupy niches on their island or islands that are occupied by other species in mainland environments. Thus, they are especially vulnerable to invasion from mainland species. For example, the famous woodpecker finch (*Camarhynchus pallidus*) of the Galapagos Islands would be unlikely to retain its feeding niche (removing invertebrates from the bark of trees with a cactus spine) if it had to compete directly with true woodpeckers (Family Picidae). Island species also have no evolutionary exposure to mainland predators, competitors, and diseases, and so are vulnerable to invasions of such species. Given these ecological predispositions to extinction, it is not surprising that the rates of island extinctions have been high. Even expressions like "dead as a dodo" (a reference to a large flightless pigeon (*Raphus cucullatus*) of the island of Mauritius exterminated by humans and their associated introductions of pigs, rats, and cats by the eighteenth century) underscore how pervasively island species epitomize the extinction process, and how many of these species have already been lost. If island species are to survive, conservation strategies must preserve critical island habitat, eliminate introduced competitors and predators, and protect island species from human hunting, collection, and disturbance.

4.6. The Problem of Application: How Do We Manage Biodiversity?

4.6.1. The Problem with "Hotspots"

Global resources exist to help locate and define which species are in need of special protection. Foremost among these is the World Conservation Union's "Red List" (http://redlist.org). A species may be placed on this list in one of six categories: (1) extinct, (2) extinct in the wild, (3) critically endangered, (4) endangered, (5) vulnerable, or (6) near threatened. However, no list ever protected anything, and no species on the Red List's Category One list can now be saved. For the species that remain, protection must be accomplished by first identifying where threatened species live, determining what measures must be taken in those areas to ensure their survival, and then finding people with the will, influence, resources, and authorization to carry out the plan.

The world ***hotspots*** are a first approximation of the location of priority areas for biodiversity conservation, but their boundaries are too coarse for setting practical and specific conservation goals. In addition, most hotspots have lost most of their original habitat, so managers must concentrate on what remains, which often makes conservation efforts highly site-specific (Harris et al. 2005). Further, managers must often make quick decisions with incomplete information. What tools can they use to make the best possible decisions in less than ideal circumstances with limited time, resources, and information?

4.6.2. Identifying Areas of Conservation Value Using Remotely Sensed Data

The rapid rate of habitat destruction in many parts of the world sometimes makes historical sources of data that were the original basis for site specific protection obsolete. Biologists Grant Harris, Clinton Jenkins, and Stuart Pimm noted that "…[older] maps of historical species richness identified priority areas that are no longer forested, with little or no biodiversity left to conserve" (Harris et al. 2005). To solve this problem, they developed a three-step method for identifying areas of conservation priority. First, they mapped an area of interest (in this case, a remnant of Brazil's Atlantic Forest) using a Landsat Thematic Mapper, a software that can process satellite image data. Then, using predictions generated from the mapper of areas and locations of remaining intact forests, supplemented with data on bird species' ranges and elevations, they determined a subregion with the highest density of threatened birds. Lastly they refined conservation priorities to one habitat type and selected eight sites predicted to be rich in threatened species. This approach is cost-effective because habitat losses within hotspots make discriminating choices of individual sites a prerequisite to effective conservation, leading the authors to conclude "Many conservationists wish to preserve the entire land area of biological hotspots, which are rich in species but low in habitat, such as the Atlantic Forest Region of Brazil. Although conservation wants the lot, funding, politics, and the amount and spatial extent of remaining forests complicate this goal.… Refining hotspot conservation means identifying specific locations (individual habitat patches) of realistic size and scale for managers to protect and politicians to support (Harris et al. 2005:1967).

4.6.3. Tracking Biodiversity Using Indicator Species

4.6.3.1. Biodiversity Indicators: Using "Surrogate" Species as Biodiversity Indices

An ***indicator***, or ***surrogate species*** is one who status is assumed to reflect the status of other species with which it shares the community and may be defined as "an organism whose characteristics, such as presence or absence, population density, dispersion, or reproductive success are used as an index of attributes too difficult, inconvenient, or expensive to measure" (Landres et al. 1988). Indeed, exactly what an indicator species "indicates" varies in different contexts. No less than seven different kinds of "indicator species," each "indicating" something different, have been described by various authors (Lindenmayer et al. 2000). The problem that managers must solve with respect to indicator species is twofold. First, can they identify an indicator species that indicates anything meaningful about biodiversity? Second, what aspect of biodiversity should they attempt to measure with an indicator species? Let us explore some practical dimensions of its applications with a real study.

In California's (USA) coastal sage scrub vegetation, a relatively rare and ecologically sensitive habitat that has diminished in the advance of human development, Chase et al. (2000) attempted to determine if the presence of *any* individual bird or small mammal species found in this habitat at a particular sampling point was correlated with increased species richness at those same points. The results were disappointing. For one thing, any species found at all sites, all but one site, or only one site could not serve as an indicator species. These criteria eliminated 21 of 37 potential species, including two species of conservation concern, the Loggerhead Shrike (*Lanius ludovicianus*) and the Stephens' kangaroo rat (*Dipodomys stephensi*). Both were detected at only one site. Thus, the authors concluded, "species of conservation concern cannot be assumed to be indicators of "hotspots" of bird and mammal species richness in coastal sage scrub" (Chase et al. 2000). The authors concluded that "efforts to conserve bird and small mammal biodiversity in coastal sage scrub should not focus exclusively on rare species … but instead should focus on a diverse suite of species that are representative of the range of variation in communities found in coastal sage scrub habitats" (Chase et al. 2000). These words reflect the study's results, but advising managers to assess biodiversity by sampling everything forgets the original reason for trying to determine an indicator species in the first place. The problem remains. What alternatives exist?

4.6.3.2. Taxon-Based Biodiversity Indicators

Taxon-based indicator species, or "taxon surrogates," as they are sometimes called, are those whose presence or absence is correlated with significant changes in biodiversity in a particular taxonomic group. That is, an estimate of species richness of a designate group, such as reptiles, is predicted by using a surrogate variable that is more easily estimated or already known from previous studies, such as family richness. A taxon-based indicator approach has the potential for wider applicability than a single indicator species approach because, instead of relying on a particular species, with an equally particular range and distribution, it relies instead on the existence of a relationship between richness in the same group of organisms at lower and higher taxa (for example, a positive correlation between species richness and family richness in the same group), and therefore could be used in any locality. Although an intuitively appealing and attractive concept, the success of this approach in actual investigations has been mixed. Let us look at one example.

Mexico is one of the world's 17 "megadiversity" countries which contain 66–77% of the world's known species (Gaston and Spicer 2004:89). In Mexico, virtually all of the world's biomes are represented, and floristic richness is estimated to be between 22,000 and 30,000 species. In this setting, plant taxonomist Jose Villaseñor and his colleagues attempted to apply a surrogate approach by using existing inventories of local and regional floral to see if richness in higher taxa could be used as a predictor of species richness in vascular plants (Villaseñor et al. 2005). They found that accuracy depended on both taxon and vegetation type. When all families of vascular plants were considered together, variation in plant genera richness explained 85% of variation in species richness. Explanatory power increased if the analysis was restricted to a particular vegetation type, in which case genera richness could explain up to 95% of variation in species richness. Unfortunately, many existing inventories and other databases do not specify to the level of genus, but only to family, and family richness was a less reliable indicator, explaining only 64% of variation in species richness. Villaseñor et al. believe that, based on previous studies in Mexico, about 77% of plant families in a newly-studied area can be identified within 2 years, and such identification can be accomplished in less time if the inventory is focused on identifying plants only to the family level from the start. Regarding the ability of this approach to predict species richness in new areas, they asserted that "higher taxon/species function may be highly predictive, particularly when analyses are restricted to ecologically homogeneous regions … and when curves are custom-fitted to particular regions" (Villaseñor et al. 2005:237).

If a taxonomic surrogates can work for one group of organisms (vascular plants), in one country (Mexico), would it be possible to combine family indices of different kinds of organisms to produce an aggregate biodiversity index for arbitrarily defined regional grid cells that could be mapped worldwide? Williams et al. (1997) attacked the problem by combining family richness in four major organism groups; plants, amphibians, reptiles, and mammals. Their choice of these groups was based on: (1) the need to limit the number of groups to keep the index from becoming unmanageable; (2) the popular appeal and established efforts to conserve species in these groups; and (3) the availability of reliable regional information for these groups. Williams et al. divided the world into grid cells of 611,000 km^2 at intervals of 10° longitude, and then, using a variety of existing data sets, calculated three measures of "family richness" for each cell. *Absolute family richness* was obtained by summing local family richness counts (number of families in the grid cell) for each of the four groups according to the formula

$$\textit{Absolute family richness} = f_{p,1} + f_{a,1} + f_{r,1} + f_{m,1}$$

where f is the number of families in each group, designated by subscript (i.e., p for plants, a for amphibians, r for reptiles, and m for mammals). *Proportional family richness* is determined by summing the local *proportion* of family richness in the different major groups through the formula

$$\textit{Proportional family richness} = (f_{p},{}_{1}/F_{p}) + (f_{a,1}/F_{a}) + (f_{r,1}/F_{r}) + (f_{m,1}/F_{m}).$$

The new term in this formula, F, represents the total worldwide number of families in each group. Thus, it effectively equalizes the contributions of groups with different numbers of families and therefore weights the index to favor areas that have a greater proportion of the families in each group, not simply the areas that have the greatest number of families. A third measure, *proportional family richness weighted for species richness*, is calculated as

$$S_p(f_{p,1}/F_p) + S_a(f_{a,1}/F_a) + S_r(f_{r,1}/F_r) + S_m(f_{m,1}/F_m).$$

The new term, S, is the total number of species in each group (Williams et al. 1997).

Using this method, Williams et al. found a pattern of increasing diversity with decreasing latitude and close correlation of the three indices with one another (0.949–0.991 in Spearman's rank correlation coefficients). Given the correlation of results, it is not surprising that the methods made similar identifications of regions with high biodiversity (Figure 4.16). Central and southern Columbia, Nicaragua, Oaxaca (southern Mexico), and southern peninsular Malaysia all were identified as biodiversity "hotspots" in at least two of the three methods.

Taken as a specific case, the approach used by Williams et al. has obvious faults, the most blatant of which is its exclusion of groups that are far more species rich than those chosen. Williams et al. excluded, among other things, insects, fungi, and bacteria. The study also does not tell us if patterns of biodiversity at the family level are similar at higher levels, such as orders or classes. However, the indices derived do provide estimates of diversity that cover a broad range of groups of conservation concern, and the method can be applied to other groups as the reliability of data improves and as conservation efforts expand to be more intentional in including other taxa.

4.6.3.3. *Structure- and Function-Based Biodiversity Indicators*

Structure-based indicators attempt to index changes in biodiversity through assessing changes in ecological structure (Lindenmayer et al. 2000). Such indicators are appealing in habitats where one or more elements, such as vegetation, are structurally complex. For example, in forest ecosystems, structural elements such as stand complexity and foliage height diversity have been used as indices of biodiversity. Other indicators, applicable to a variety of habitats, include measures of connectivity and heterogeneity. Structure-based biodiversity indicators may be appealing because, in many cases, they can be shown to reflect changes in ecosystem processes or patterns. In contrast, ***function-based indicators*** of biodiversity assume that, in any community, some species are "drivers" and some are "passengers" in the ecologic process. The function-based indicators are the "drivers" that determine the characteristics of the ecosystem in which they live because of ecological functions that they perform in the system. The passengers "ride along" on the effects created by the drivers.

Driver species are analogous to the more familiar concept of "keystone species," species that have disproportionate effects on community or ecosystem processes and, as a result, disproportionately affect biodiversity. The American

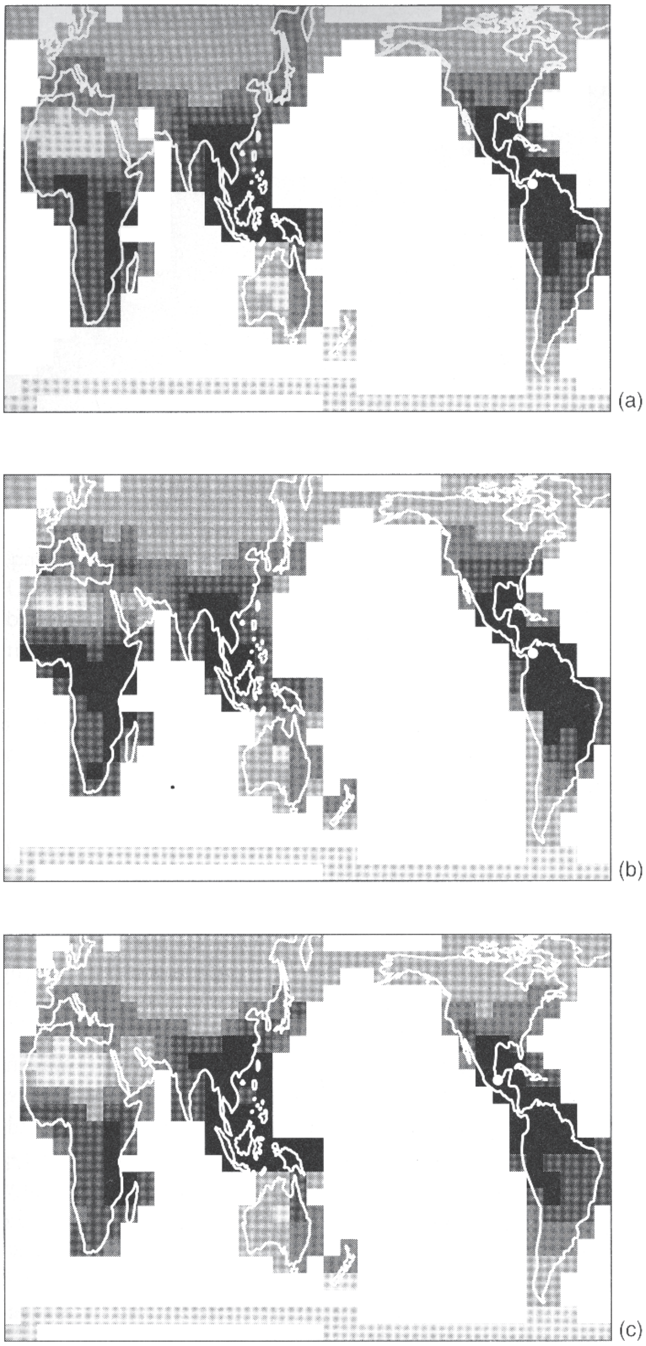

FIGURE 4.16. Maps of combined family richness of terrestrial and freshwater seed plants, amphibians, reptiles and mammals worldwide on an equal-area grid map (grid-cell area *ca.* 6,111,000 km^2, for intervals of 10° longitude. Maps produced by summing (a) absolute family richness; (b) proportional family richness; and (c) proportional family richness weighted for species richness. Maximum scores shown in black, other scores divided into five gray scale classes of approximately equal size based on numbers of grid cells. Although units and numerical values differ, frequency classes are comparable among maps. (Courtesy of Williams et al. 1997, Figure 1, p. 144, Royal Society of London.)

FIGURE 4.17. The North American bison (*Bison bison*) is an example of a "keystone species" which, through a variety of effects including grazing, trampling, wallowing, and deposition of feces and urine, changes the biodiversity of a community, as well as its vertical and horizontal structure and heterogeneity. (Photo courtesy of U.S. Geological Service.)

bison (*Bison bison*) provides an excellent case history of the specific mechanisms through which ***keystone species*** mediate biodiversity levels by altering ecosystem function (Figure 4.17).

4.6.3.4. *Bison as an Example of a Function-Based Keystone Species*

As bison move in herds through a prairie, their urine and feces create elevated levels of nitrogen in distinct patches, altering the gradient of a vital plant nutrient, raising the level of habitat heterogeneity, and increasing overall biodiversity at both alpha and beta levels (Steinauer and Collins 1995). By consuming nitrogen stored as amino acids in plants and returning more labile forms of nitrogen to the soil in the form of urine and feces, bison increase the rate of nitrogen recycling in the system. This increase affects plant growth rates (Risser and Parton 1982), production (Steinauer and Collins 1995), efficiency of water use by plants, and plant community composition (Risser and Parton 1982). Overall, the urine and feces deposition of bison on prairies forms distinct habitat patches recognizable at both species and community levels (Steinauer and Collins 1995).

Bison also exert strong effects on biodiversity through grazing because they preferentially graze dominant C_4 grasses (grasses that use 4-carbon rather than 3-carbon pathways in photosynthesis) such as big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachyrium scoparium*). Reduction in these dominant grasses increases densities and diversities of forb species that are a less important component of the bison's diet. Such effects are particularly important after a fire because C_4 grasses tend to dominate prairie sites after burning if grazing does not occur. In an experimental analysis of these effects, Hartnett et al. (1996) found an average of 40 species on sites grazed by bison, but only 29 species on ungrazed prairie sites.

In addition to effects mediated by grazing, bison affect alpha and beta diversity levels by trampling and wallowing. "Wallows" are small depressions in grasslands, often associated with moist sites, that are created when bison trample the ground and roll in the exposed soil (Polley and Collins 1984). Wallowing creates openings in grasslands with different soil textures, levels of soil moisture, pH, and available phosphorus, among other variables, creating conditions that lead to increased beta diversity in the landscape. These environmental gradients occurring over a relatively small spatial scale lead to assemblages of plant species in the wallow that are very different from the surrounding prairie. However, the effects of bison activities favor increased diversity of prairie vegetation rather than invasion by non-prairie vegetation. The physical action of trampling and rolling in the wallow by bison tends to break and crush woody vegetation that could invade such sites, thereby reducing encroachment by woody vegetation into prairie communities (Polley and Collins 1984).

A third effect of bison occurs through interactions with other species. Bison and prairie dogs (*Cynomys* spp.) form mutually beneficial grazing associations in mixed-grass prairies. Feeding preferentially at the edge of prairie dog colonies (Kruegar 1986), bison reduce forage biomass and density, making it more difficult for terrestrial predators to approach the colony without being seen. Prairie dogs, through their grazing activities at the colony's edge, create microenvironments of more vigorous plant growth preferred by bison. The combined effects of bison-prairie dog grazing lead to higher shoot-nitrogen concentrations in plants than in the surrounding prairie (Kruegar 1986). These activities help keep the interior of the colony free from vegetation, more amenable to burrowing, and more difficult for predators of prairie dogs to use without being detected.

Identifying keystone species allows conservation biologists to concentrate management efforts on those species that have the greatest effect on overall community and landscape biodiversity and to imitate and influence the processes and actions of keystone species that lead to increased biodiversity. But saying that we should concentrate on conserving keystone species fails to understand a manager's dilemma. How, exactly, do we identify a keystone species and its effects?

4.6.3.5. *Ecological Redundancy and Function-Based Biodiversity Indicators*

Conservation biologist D. H. Walker offers a four-step approach integrated in the concept of ***ecological redundancy***. Walker asserts that the key question to ask is "how much, or rather, how *little*, redundancy is there in the biological composition of systems?" (Walker 1992). First, determine the functionally different kinds of organisms in the ecosystem. That is, what are the rate-limiting processes in the system and which species are involved in which processes? Second, determine the number of species in each functional group. If a group has only a few species (low redundancy) it should receive priority over a group with many species (high redundancy). Third, examine interactions among species in each guild. There is functional redundancy if the loss of one species is compensated by an increase in density of another species. Finally, consider the relative importance of each functional group in ecosystem maintenance. Groups that perform functions considered more essential would be given conservation priority over groups that perform less essential functions.

A function-based approach of identifying indicator species can help managers make correct decisions about conservation priority based on objective criteria. The weakness of such an approach is that it requires extensive and detailed information to correctly identify an ecosystem's functional groups and the species within them.

Managers have no "magic indicators" that provide precise assessments of biodiversity with minimal effort. But managers must still manage. What are constructive approaches to managing of biodiversity even when available information is incomplete?

POINTS OF ENGAGEMENT – QUESTION 1

It is not possible to assess, manage, or preserve all biodiversity in a system or management unit. It may not even be desirable. Based on available techniques and approaches, what do you now think would be the "best" way for a manager to evaluate biodiversity and what criteria would you use for the manager to determine when "enough" diversity is being effectively managed and preserved?

4.7. The Problem of Conservation: How Do We Identify and Prioritize Areas to Preserve Biodiversity?

4.7.1. Current Global Prioritization Strategies

Today there are identifiably nine major global biodiversity conservation strategies, or, more precisely, templates for identifying and selecting land areas to conserve for biodiversity. These are: (1) the *Crisis Ecoregion* (CE) strategy, which prioritizes conservation of ecosystems facing the highest threats of destruction and degradation; (2) *Biodiversity Hotspots* (BH), which selects landscapes with the highest species diversity per unit area; (3) *Endemic Bird Areas* (EBA), which prioritizes areas with the highest densities of endemic bird species; (4) *Centers of Plant Diversity* (CPD), which targets areas with exceptional plant diversity per unit area; (5) *Megadiversity Countries* (MC), which identifies nations with the highest levels of biodiversity, and designs conservation plans sensitive to national interests and boundaries; (6) *Global 200 Ecoregions* (G200), a science-based global ranking of the Earth's most biologically outstanding terrestrial, freshwater and marine habitats; (7) *High Biodiversity Wilderness Areas* (HBWA), a strategy that identifies areas that combine high levels of biodiversity, relatively low human population density, and high landscape connectivity; (8) *Frontier Forests* (FF), a strategy targeting the world's remaining large intact natural forest ecosystems; and (9) *Last of the Wild* (LW), a strategy that places conservation priority on areas representing the largest and relatively "wildest" (lowest human population and environmental impact) places in each of their biomes (Brooks et al. 2006). Each of these strategies uses a somewhat different approach to biodiversity conservation, with unique, and, sometimes, complementary strengths and weaknesses. However, all can be conceptually understood in terms of two criteria. First, such templates can be classed as proactive versus reactive, and, second, they emphasize either irreplaceability, which focuses on rarity and uniqueness, or vulnerability, which focuses on threat (Figure 4.18). For example, CE is a highly reactive strategy, prioritizing conservation areas according to immediate threat, while HBWA is highly proactive, attempting to conserve areas that are still relatively unaffected by negative

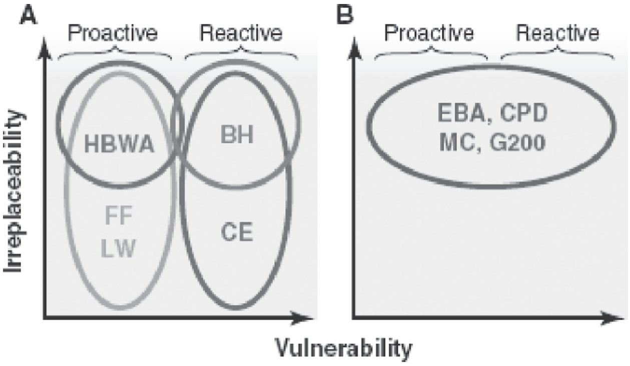

FIGURE 4.18. Global biodiversity conservation priority templates placed within the conceptual framework of irreplaceability and vulnerability. (A) Reactive approaches focus on the protection of areas of high vulnerability and immediate threat. Proactive approaches focus on areas with high biodiversity still relatively unaffected by human influence. (B) Four approaches that do not incorporate vulnerability as a criterion, but consider only irreplaceability (uniqueness) in conservation. Abbreviations explained in text. (From Brooks et al. 2006. Global biodiversity conservation priorities. *Science* 313:58–61. Reprinted with permission of AAAS.)

human influences. In contrast, conservation templates that focus on endemic species, such as EBA, use irreplaceability (endemic birds occur in only one place or region) as the guiding criteria to prioritize conservation areas. Some strategies, such as those that focus on endemic species or biodiversity alone, consider only irreplaceability, not vulnerability. What is important to note is that templates that prioritize the same thing, such as high vulnerability, tend to place priority of conservation effort on many of the same areas, while those that prioritize different things (for example, irreplaceability versus vulnerability) have much less overlap in their selection of priority conservation areas (Figure 4.19). Seventy-nine percent of all land on Earth is prioritized in at least one of these systems, but the different templates require different kinds of conservation approaches. A strategy that prioritizes wilderness areas of high biodiversity is amenable to landscape level management practices at large spatial scales that can be applied over fairly long time periods, while a strategy that prioritizes irreplaceability and threatened species must often act quickly and effectively at specific sites.

Global conservation priority strategies are effective at raising money because they offer easily identifiable targets that attract the support of large donors. However, the same strategies have often failed to inform or affect actual conservation management and implementation, precisely because they are not designed to address it. It is important for conservation biologists to understand the foundations of these global approaches so that they can self-reflectively decide which one is most appropriate for particular conservation problems. But it is also essential that they move beyond generalized global strategies to landscape- and site-specific management plans that can really conserve biodiversity.

4.7.2. Management Approaches to Biodiversity at Landscape Levels

4.7.2.1. Gathering Appropriate Background Data

A first step in conserving biodiversity is to appreciate a spatial scale perspective for alpha and beta diversity. Specifically, if the goal is to maximize local diversity at a single site (alpha diversity), choose a site with high species richness. But what if the management objective is to maximize biodiversity at a regional level (beta diversity)? In that case, a strategy of simply reserving all sites with the highest levels of species richness will have little value if different areas contain the same species. Most sites are dominated by generalist species, even sites with high levels of species richness. Ecological specialists may occur at sites with relatively low species richness. At regional levels, the key is not to select the sites with highest richness, but to select sites in which species compositions are *most dissimilar to one another*. By protecting areas of less biologic similarity, protection of regional endemic species and ecological specialist species is enhanced, and these contribute most to biodiversity at regional levels.

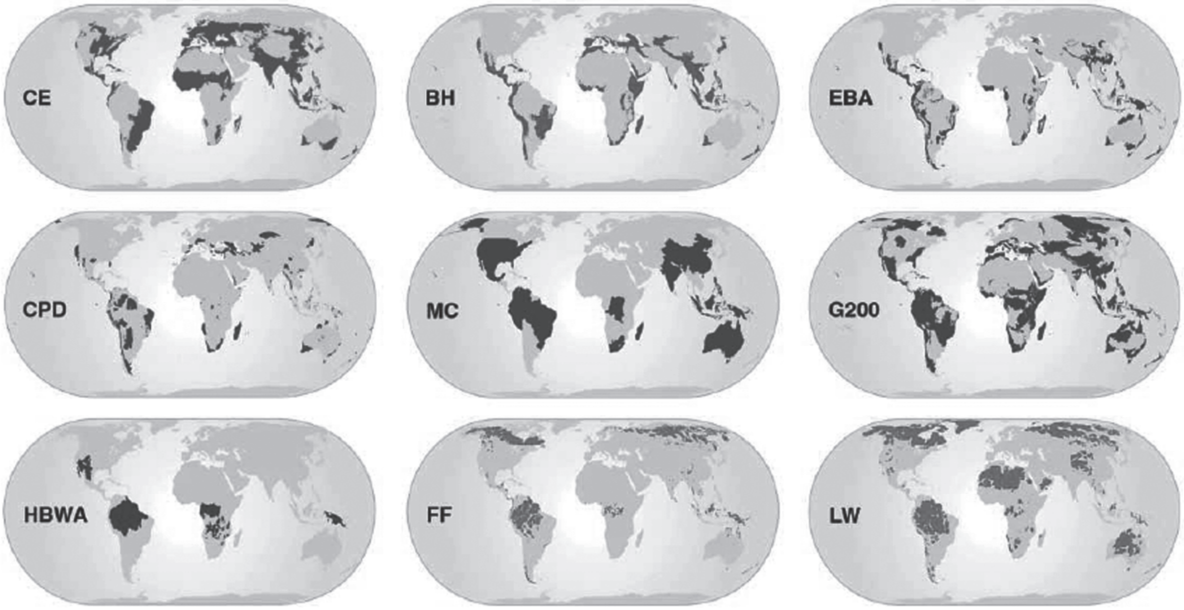

FIGURE 4.19. Maps of nine global biodiversity conservation priority templates. Abbreviations explained in text. (From Brooks et al. 2006. Global biodiversity conservation priorities. *Science* 313:58–61. Reprinted with permission of AAAS.)

4.7.2.2. Maintaining Ecological and Evolutionary Processes Promoting Biodiversity

Although accurate inventories of diversity are important, biodiversity is neither maintained nor managed simply by counting biological "things." The processes that shape biodiversity, although they may operate over long time spans, can still be appropriate subjects of intentional conservation management. The most important among these processes include *maintenance of gene flow*, *creating resources for habitat and niche specialization*, and *maintaining effective population sizes*.

Gene flow between population subunits is maintained by connectivity between subunit locations. In cases where physical connections between population subunits, such as habitat corridors, can enhance connectivity (movement and interchange of individuals) between population subunits, managers may be able to increase gene flow between population subunits at varying spatial scales. More specific considerations of how this is done will be considered in chapters that follow on genetics (Chapters 6 and 7), populations (Chapters 8 and 9), and habitat and landscape conservation (Chapter 10). *Creating resources for habitat and niche specialization* requires a manager to have knowledge of species-specific needs, and the skills to meet them. Various forms of habitat alteration, including, where appropriate, such techniques as prescribed fire, permanent, periodic, or seasonal flooding, alteration and removal of vegetation, or addition of key resources (for example, nest site structures) can, when intelligently applied, increase resources for niche specialization, contributing to an environment in which more species, especially those with more specialized needs and preferences, can persist. Particular techniques, and case histories that illustrate them, will be examined in greater detail in Chapter 10 in our study of habitat and landscape conservation.

Maintaining effective population sizes permits resident populations to retain genetic diversity and corresponding environmental adaptability. Making accurate and precise estimates of what constitutes an effective population size requires knowledge of a species mating system as well as the number of individuals present. The methods for making such estimates will be an important focus of our examination of conservation genetics in Chapters 6 and 7.

4.7.2.3. Regional Biodiversity Management – Defining Functional Conservation Areas

Because the distribution of global biodiversity is complex, mapping and protecting key areas requires taxon specific approaches, careful conceptual methods, and sophisticated technologies for spatial problem solving. Poiani et al. (2000) have addressed this problem through the development of "functional conservation areas." By examining biodiversity at different spatial scales (Figure 4.20), Poiani et al. (2000) define ecosystems and species at four different levels: local, intermediate, coarse, and regional. Within these levels, functional conservation areas (FCA) are identified as "a geographic domain that maintains focal ecosystems, species, and supporting ecological processes within their natural range of variability" (Poiani et al. 2000). FCAs are delineated as sites, landscapes, and networks. Functional sites conserve one or more endangered species or rare ecosystems, typically at a local scale. Functional landscapes encompass full terrestrial and aquatic habitat gradients and a diversity of ecological processes needed to maintain those gradients and the species that live within them. Functional networks provide "spatial context, configuration,

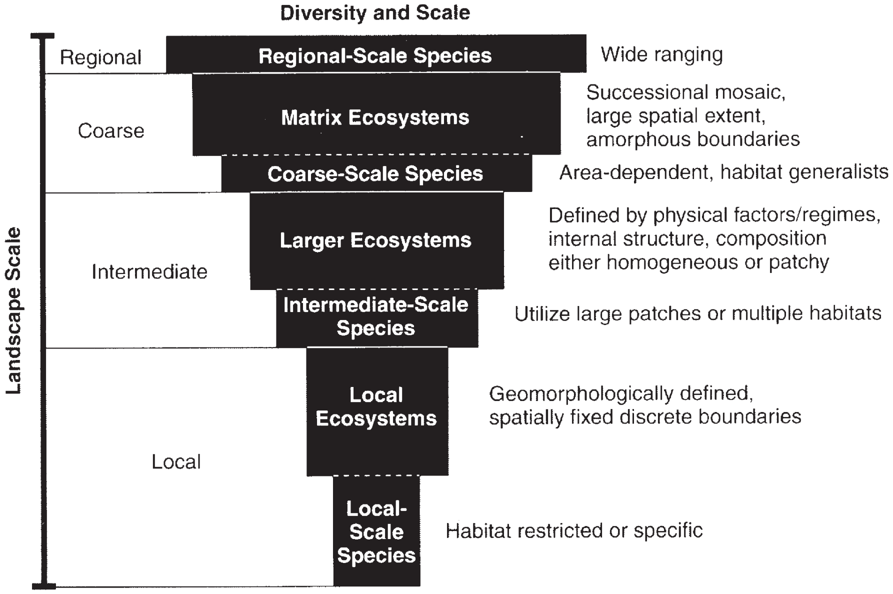

FIGURE 4.20. A method of categorizing biodiversity at regional, coarse, intermediate and local geographic scales. (Poiani et al. 2000. Copyright American Institute of Biological Sciences.)

and connectivity to conserve regional scale species with or without explicit consideration of biodiversity at finer scales" (Poiani et al. 2000). A similar approach has been developed by Jonathan Higgins and his colleagues for classifying aquatic systems. They begin classification of biodiversity with determination of an ***aquatic zoogeographic unit*** (AZU), essentially a watershed, which serves as the overall planning unit. Within an AZU are one or more ***ecological drainage units*** (EDUs). Within a single EDU are multiple ***aquatic ecological systems*** (AESs). Within a single AES, macrohabitats can be managed specifically for individual species or species groups (Higgins et al. 2005). Using GIS, Higgins et al. created an inventory of mapped and classified units that can be used to identify and differentiate spatial patterns of aquatic ecosystems. Conservation planning and priorities are then developed to preserve a diversity of system types, rather than simply individual populations. We will explore this approach in more detail in our examination of conservation of aquatic habitats (Chapter 11).

POINTS OF ENGAGEMENT – QUESTION 2

Many US conservation laws are either species-based (e.g. Endangered Species Act, Marine Mammal Protection Act) or impact-based (National Environmental Policy Act, Clean Water Act). None are designed primarily to protect biodiversity *per se*. What would be the value of a conservation statute written explicitly to protect biodiversity, and why might it require "functional conservation areas" as management units to be effective?

Regional and landscape conservation criteria, however well conceived, are even more valuable if complemented with reliable information on species, habitat and ecosystem distributions at multiple scales. Thus, conservation of biodiversity increasingly turns to Geographic Information Systems (***GIS***) and the related Gap Analysis Program (GAP analysis, Chapter 10) to supply information necessary for intelligent management and conservation decisions. GIS systems can organize and overlay thematic data, such as soils, vegetation, hydrology, and dominant vegetation, within a defined area, and then relate such data, along with land use patterns and locations of existing nature reserves, to the distribution of endangered or endemic species (Scott et al. 1987). Using such a technique, conservation biologists and land use planners can determine: (1) what proportion of an area's biodiversity is protected in an existing distribution of nature preserves and under existing land use practices; (2) whether such protection can be expected to permit the persistence of endangered or endemic species; and (3) the best location and arrangement of new nature preserves or the best areas to attempt to change current land use patterns. Only when conservation biologists effectively integrate global patterns of biodiversity, taxon- and site-specific variations, well-organized conceptual frameworks for biodiversity protection, and technologically advanced data analysis and land use planning toward the goal of protecting biodiversity at multiple scales is there reasonable hope that biological diversity will persist in any area or ecosystem.

4.7.3. Building Biodiversity Conservation into Existing Management Plans – The New South Wales Environmental Services Scheme

In most real-world management settings, biodiversity conservation cannot be treated as a separate management program independent of existing and ongoing environmental management that must consider other needs and priorities. But biodiversity conservation can be incorporated into existing management schemes, with the aid of managerial creativity. An outstanding example of the latter can be found in the efforts of environmental managers in Australia's New South Wales (NSW) province. In 2002, the NSW Department of Natural Resources launched the Environmental Services Scheme (ESS), a comprehensive management effort that would provide financial incentives to private landowners who would undertake changes in land use or management that would improve the status of environmental services (i.e. benefits derived from healthy ecosystem function). However, the budget for incentives was limited, and there were more applicants that there was money to satisfy them. How would managers determine which landowners were most deserving of payment? As is often the case, this necessity mothered the invention of metrics that could "score" benefits of changes in land use or management by the landowner relative to a range of environmental services (Oliver et al. 2005). One such service was enhancement of biodiversity.

The Department developed a metric known as the Biodiversity Benefit Index (BBI) which was derived from two other metrics, a Land Use Change Impact Score (LUCIS) and a Biodiversity Significance Score (BSS). The value of the LUCIS is the difference between scores assigned to present vegetation condition (VC_{t1}) and future vegetation condition (VC_{t2}) (Table 4.10), plus the difference between the associated conservation significance (CS) of present and future vegetation condition (Table 4.11), or

$$LUCIS = (VC_{t1} - VC_{t0} + CS_{t1} - CS_{t0})/2$$

Thus, the value of LUCIS is positive if a management action improves vegetation condition and its significance to conservation. Highest VC scores were given to sites that showed high plant species richness and vegetation and to communities that protected native endangered plant species.

The Biodiversity Significance Score was constructed from VC and CS scores, plus a third metric called Landscape Context (LC). The landscape context of sites was related to their contribution to biodiversity at regional, local, and site-specific levels, with highest scores going to areas that increased connectivity

TABLE 4.10. Vegetation condition assessment categories used as part of the New South Wales (Australia) Environmental Services Scheme that quantified the value of on-site biodiversity through the Biodiversity Benefits Index.

Vegetation Condition	Maximum Score
Richness of benchmarked plant groups (20 × 20 m plot for ground cover, 20 × 50 m plot for woody vegetation)	25
Cover of benchmarked plant groups (20 × 20 m plot for ground cover, 20 × 50 m plot for woody vegetation)	20
Evidence of woody species recruitment (per 20 × 50 m plot)	10
Percentage cover of exotic ground cover species (per 20 × 20 m plot)	15
Percentage cover of organic litter (per 20 × 20 m plot)	5
Density of large trees (per ha)	15
Density of hollow-bearing trees (per ha)	5
Wood load (lineal metres of logs per ha)	5

Source: Oliver et al., The NSW Environmental Services Scheme: results for the biodiversity benefits index, lessons learned, and the way forward, *Ecological Management and Restoration*, Copyright 2005 by Blackwell Publishing.

TABLE 4.11. Conservation significance assessment categories used as part of the New South Wales (Australia) Environmental Services Scheme that quantified the value of on-site biodiversity through the Biodiversity Benefits Index.

Decline In Preclearing Distribution %	Category	Score
	Non-native vegetation	0
< 30	Native– least concern	20
30–50	Native– near threatened	40
50–70	Native– vulnerable	60
70–90	Native– endangered	80
> 90	Native– critically endangered/presumed extinct	100

Source: Oliver et al., The NSW Environmental Services Scheme: results for the biodiversity benefits index, lessons learned, and the way forward, *Ecological Management and Restoration*, Copyright 2005 by Blackwell Publishing.

TABLE 4.12. Landscape context assessment categories used as part of the New South Wales (Australia) Environmental Services Scheme that quantified the value of on-site biodiversity through the Biodiversity Benefits Index.

Landscape Context Assessment	Maximum Score
Regional context (biodiversity priority areas, regional corridors, etc.)	10
Local context:	
Area of patch of native vegetation of which assessment area is part	25
Native vegetation within the neighbourhoods 100, 1,000, 10,000 ha	25
Distance to core area of native vegetation patch greater than 50 ha	10
Site context:	
Assessment area is adjacent to existing remnant	6
Assessment area connects two or more remnants	6
Assessment area incorporates a riparian zone	6
Assessment area contains large trees	6
Assessment area has a large area to perimeter ratio	6

Source: Oliver et al., The NSW Environmental Services Scheme: results for the biodiversity benefits index, lessons learned, and the way forward, *Ecological Management and Restoration*, Copyright 2005 by Blackwell Publishing.

between remnant native vegetation, protected riparian zones or large trees, contained native vegetation in large areas with minimal edge, or had been identified as important for regional biodiversity (Table 4.12) Obviously, because no one area could receive a perfect score in every LC criteria and almost all areas received a unique, site-specifc score, the metric provided managers with a way to discriminate between sites. The LC was combined with VC and CS scores to determine the Biodiversity Significance Score. This was equal to

$$BSS = VC(LC + CS)/200$$

Because the maximum value for any metric (VC, LC, or CS) was 100, this equation limits the values of BSS within the range of 0–100.

It is important to realize that each index, VC, LC, and CS, was applied to a different management scale. To see how the metrics were actually implemented in assessment, follow the flowchart in Figure 4.21 as you read this explanation. Initially, department managers stratified the property of each applicant in four steps. After an initial review of the application and the perceived value of the owner's property in a regional landscape context, managers identified "management units" on the property which shared the same past, present, and proposed land use. Each management unit was then scored through a Landscape Context Assessment. Within each management unit, managers identified "assessment units" which were areas that shared the same vegetation communities. Assessment units were then scored according to a Conservation Significance Assessment. Finally vegetation condition in assessment units was sampled directly by placing survey plots in the assessment units, and data from survey plots was used to compute the Vegetation Condition Assessment.

Once the LUCIS and the BSS were known, the Biodiversity Benefits Index can be determined as

$$BBI = LUCIS \times BSS$$

Thus, if both LUCIS and BSS attained their maximum scores of 100, the maximum value of a site-specific Biodiversity Benefits Index was 10,000 per ha. Most scores averaged between 0 and 200, depending on land use and management changes (Figure 4.22). Once the BBI

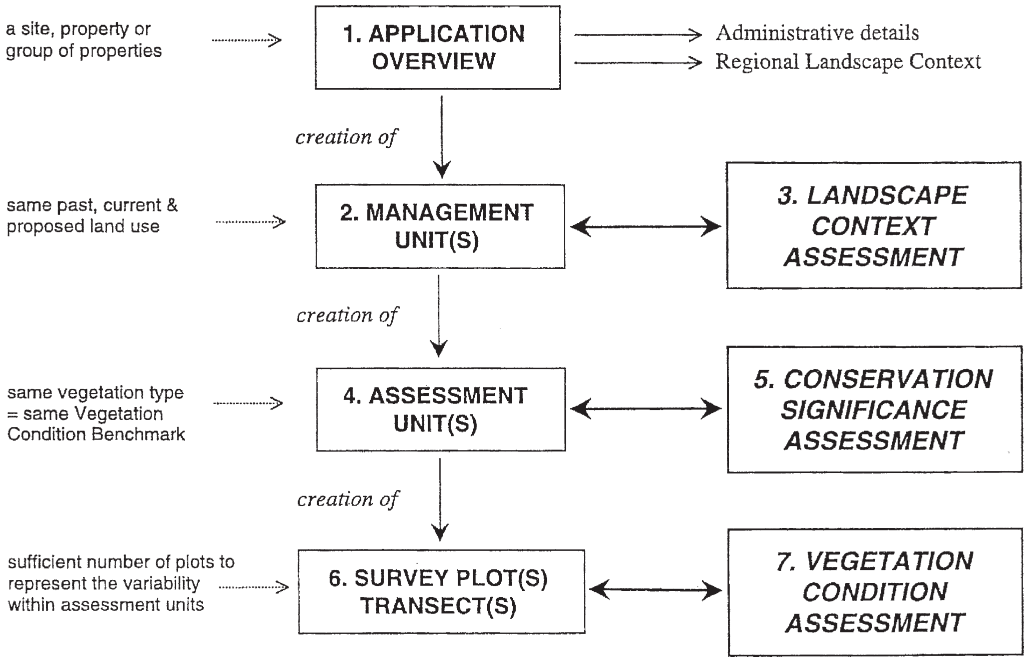

FIGURE 4.21. Overview of the steps involved in the stratification of each assessed property and data collected at each level to create the Biodiversity Benefits Index used in the New South Wales (Australia) Environmental Services Scheme. (Oliver et al., The NSW Environmental Services Scheme: results for the biodiversity benefits index, lessons learned, and the way forward, *Ecological Management and Restoration*, Copyright 2005 by Blackwell Publishing.)

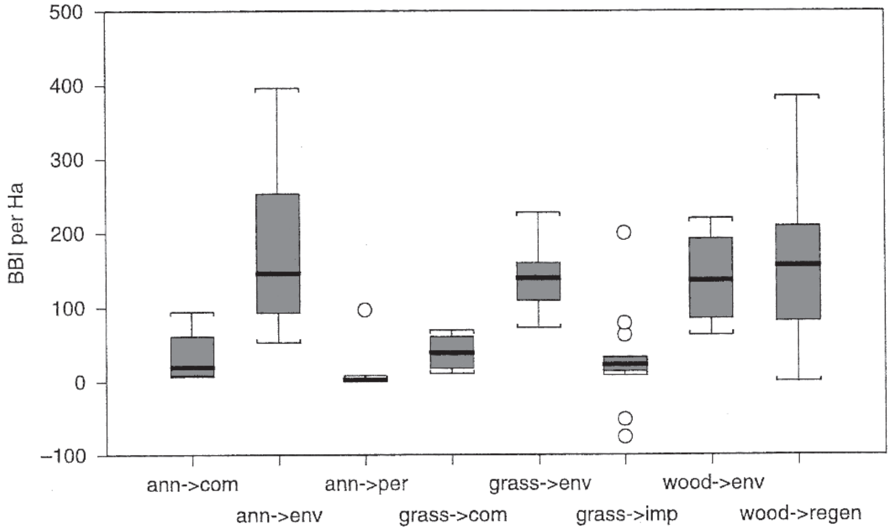

FIGURE 4.22. Scores of the Biodiversity Benefits Index per hectare grouped by land use and management change in the New South Wales (Australia) Environmental Services Scheme. Ann = annual pasture. Com = commercial plantation (trees). Env = environmental planting. Per = perennial pasture. Grass = mixed grassland. Imp = improved management (intensive management of annual, perennial, or mixed grassland). Wood = woodland remnant. Regen = regenerating woodland remnant. Arrows indicate change from initial (first symbol) to final (second symbol) condition. Medians shown as horizontal lines within upper and lower quartiles (shaded boxes). Box appendages (whiskers) encode adjacent values (largest observation ≤ upper or lower quartile ± 1.5 times the interquartile range). Outlier values beyond adjacent values shown individually as open circles. (Oliver et al., The NSW Environmental Services Scheme: results for the biodiversity benefits index, lessons learned, and the way forward, *Ecological Management and Restoration*, Copyright 2005 by Blackwell Publishing.)

is completed for an applicant, it can be used as a measure of the applicant's merit for receiving government financial incentives to improve environmental services, including, but not limited to enhanced conservation of biodiversity.

Like all metrics, the Biodiversity Benefits Index developed by the Department of Natural Resources in New South Wales is not perfect. But the BBI is nevertheless commendable on many fronts and provides a valuable model for practical considerations in managing biodiversity. First, the BBI demonstrates a way to construct a metric that can be used at different spatial scales to evaluate vegetation and landscape condition, with conservation significance, at those scales, from individual sites to large, varied properties. Second, the BBI makes an assessment of actual and projected results and values of different management actions based on the kinds of vegetation communities they are likely to produce. Third, the BBI, in an incentive program, provides government managers with the means of engaging the public in biodiversity conservation, and permits the manager to make decisions about the distribution of financial incentives that can be rationally defended and perceived as fair by the participants and the general public. Finally, the information needed to compute the BBI can be obtained in the course of other kinds of management assessments that consider management goals other than biodiversity conservation, and thus optimize manager's time while still incorporating biodiversity as an important consideration in conservation. Current and future conservation managers would do well to employ the kind of thinking and approaches characteristic of the BBI in making biodiversity conservation a more measurable, future-oriented, landscape-scale effort that constructively involves local private land owners with managers in management actions and strategies.

4.8. Synthesis

Scientific concepts, measurements, and values are not set by decree. They survive only if they are operational, testable, and open to analytical refinement. Biodiversity is one of the core concepts of conservation biology, but its persistence and value as a scientific idea are not yet assured. The concept of biodiversity requires thorough understanding and its mathematical definitions careful measurement if it is to be translated into meaningful ideas that shape conservation strategies. If biodiversity can be thoughtfully understood and articulated, quantitatively measured and tested, and carefully valued in both instrumental and non-instrumental ways, it will become an increasingly important component of conservation study, conservation law, and conservation policy.

The processes that control the level of biodiversity in ecological systems are still not well understood. The most effective future research on biodiversity will not be those studies that simply continue to measure it, but those that explore and test hypotheses about the ecological processes that shape it. Biodiversity is a concept that requires further refinement, and it cannot stand alone apart from other conservation priorities. Current measurements of biodiversity, with their emphasis on species richness and evenness, do not always reveal correlations between diversity and conservation value. New indices that address taxonomic uniqueness and ecological importance must be developed and used in conjunction with traditional measures of diversity if biodiversity is to provide meaningful information about the relative value of different community and landscape assemblages.

We will increasingly see the concept of biodiversity incorporated into the overall strategies of major global conservation organizations and into the management plans and assessments of government conservation agencies. The challenge will be to design such strategies and plans with care and insight so that they truly assess the condition of biodiversity at appropriate conservation and management scales, and not merely pay lip service to the concept of biodiversity while ignoring, or even harming, the substance of it.

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5

Biodiversity Conservation and Climate Change

> *Climate change represents a fundamentally different threat to Canada's national park system. Never before has there been an ecological stressor that raised questions about the adequacy of the system to protect representative samples of Canadian ecosystems.*
>
> Daniel Scott 2005:344

In this chapter, you will learn about:

1. **The scientific evidence for modern climate change**
2. **The current and predicted effects of climate change on biodiversity**
3. **Conservation strategies and policies to mitigate the effects of climate change in efforts of biodiversity conservation**

5.1. Climate and Climate Change

5.1.1. Why Does Climate Change Threaten Biodiversity?

In his remarks above, Daniel Scott was addressing the effects of contemporary climate change on only one nation, Canada, and only one dimension of its national conservation effort, national parks. But although his words are directed to the conditions of one country and one conservation strategy, Scott could just as easily have been speaking of every conservation strategy in the whole world. The most important threats to global biodiversity have traditionally been perceived as habitat destruction, fragmentation, and degradation; overexploitation of species; competition, predation, and displacement of indigenous species by invasive species; and disease. These threats remain obstacles to biodiversity conservation, but conservation efforts to mitigate them, even if confined to single species and individual locations, can be effective if intelligently applied. But another threat now casts an ominous shadow over all other dangers, and, if unaddressed, has the potential to overwhelm any local or regional actions, however well designed or intended, toward conservation goals. That threat is global climate change.

The idea that climate limits species' distributions is not new. In 1917, the American zoologist Joseph Grinnell, examining such diverse species are the Oregon jay (*Perisoreus obscurus*), pika (*Ochotona princeps*), rosy finch (*Leucosticte arctoa*), redwood chipmunk (*Eutamias townsendi ochrogenys*), and western meadowlark (*Sturnella neglecta*) (Figure 5.1), published his assessment of the role of climate in constraining the geographic ranges of these animals (Grinnell 1917). Grinnell did not call his work a "climate study," but noted, in his own words that "… upon the North American continent, one single factor does happen to loom up as being the most frequent delimiter of distribution, or even the ultimately effective one, in greater or lesser degree, even though other factors be effective also. This factor is temperature" (Grinnell 1917:128).

Grinnell considered temperature a *limiting* factor in species distribution, but not a *changing* factor. He, like other naturalists of that day, considered temperature and other climate factors to be stable and consistent, however restrictive they might be to a particular species. But the idea of *climate change* as a factor influencing species distribution, and, ultimately, species survival, is very new. In 1992, the distinguished ecologist Peter Vitousek wrote in his introduction to that year's *Annual Review of Ecology, Evolution, and Systematics* special issue on "Global Environmental Change," "ultimately, climate change probably has the greatest potential to alter the functioning of the Earth system; its direct effects on natural and managed systems ultimately could become overwhelming … nevertheless, the major effects of climate change are mostly in the future while most of the others are already with us" (Vitousek 1992:7).

The major effects of climate change might still be in the future, but climate change is no longer a future scenario, nor are its effects. Climate change is "with us." Climate change is, as Daniel Scott put it, a "fundamentally different threat," an "ecological stressor" that, unlike any other, raises questions about the adequacy of any conservation strategy or reserve system to protect and preserve representative biodiversity. The reason that such a description is warranted is because climate change is capable of altering the very nature of what is being preserved. As Scott went on to state in the context of addressing the problem climate change presents to national parks in Canada, "… the stated purpose of Prince Albert National Park is to 'protect for all time the ecological integrity of a natural area of Canadian significance representative of the southern boreal forest

FIGURE 5.1. Some of the species the early twentieth-century US naturalist Joseph Grinnell assessed in relation to the role of climate factors in their distribution included the pika (*Ochotona princeps*) (top), rosy finch (*Leucosticte arctoa*) (bottom left) and western meadowlark (*Sturnella neglecta*) (bottom right). (Pika and rosy finch courtesy of US National Park Service. Western meadowlark courtesy of US Fish and Wildlife Service.)

and plateau…'. Yet all six vegetation change scenarios examined … projected the eventual loss of boreal forest in this park…, suggesting that the park's mandate would be untenable in the long term" (Scott 2005:343). Because climate change alters the geographic location of suitable conditions ("climate niches") for many species, it is, in one sense, a form of habitat destruction. One survival strategy of species is therefore to move, tracking their "climate niche" as it changes location through time. But, in a world of increasing habitat destruction, fragmentation, and isolation, movement to new areas is often impeded. Thus, acting in concert with habitat destruction, climate change can create synergistic stresses that can lead a species to extinction. But climate change, even in the absence of direct habitat destruction, can alter the surrounding environmental conditions of a species so quickly that the species cannot adapt in time. Thus, climate change can lead species down a second pathway of extinction by exceeding their present environmental tolerances, altering their environment faster than their genetic resources can adapt to it. Thus, species have three choices when faced with climate change: disperse, adapt, or die.

5.1.2. What Is "Climate" and What Is "Climate Change"?

A dictionary would define "climate" as "the average course or condition of the weather at a place over a period of years" (Webster 1971:155). Thus, our first important distinction when examining climate change is the distinction between weather and climate. "Weather" refers to local, short-term changes in variables such as temperature, precipitation, wind speed, and humidity. Weather is constantly changing, but changing within a range of historical norms, cycles or fluctuations that, in the long term, are highly predictable. These long-term predictable fluctuations are what is meant by "climate."

Variations in climate, over the long history of the Earth, generally take one of four overall forms (Karl and Trenberth 2005). *Regular periodic variation* in climate is a kind of predictable change manifested in annual seasonal cycles and in longer-term regular fluctuations like the Milankovitch cycles (Figure 5.2A) which show periodic, regular variations in temperature on the Earth over periods of thousands of year. The periodicity of annual variation is due to the tilt of the Earth's axis relative to the axis of the sun, such that the directness and intensity of light changes at different points in the Earth's orbit, not because of a change in distance to the sun, but because of a change of different parts of the Earth in their angle of inclination toward the sun. The periodicity of Milankovitch cycles, in contrast, is due to longer term, but regular 22,000-year cycles caused by variations in the Earth's distance from the sun. Such changes, although capable of producing great differences in climatic variables in both space and time, are properly called "climate variation," not "climate change." Within such cycles, long-term averages of key climatic variables, such as temperature and precipitation, remain the same.

In contrast, *discontinuities*, *jumps*, *trends*, or *increasing variability* can all represent forms of *climate change*. In these cases, means of climate variables do not remain stationary. Climate discontinuities and climate jumps occur when climate variables, relative to the length of the temporal cycle, show a large change in magnitude in relatively short time spans (Figure 5.2B). After the jump or discontinuity, a new baseline emerges that is different from the old one. *Trends* (Figure 5.2C) in climate

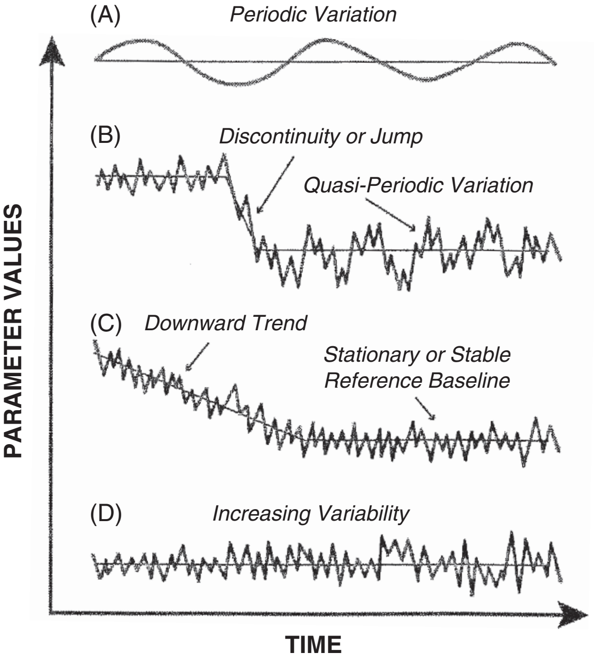

FIGURE 5.2. (A) Milankovitch cycles are examples of *regular periodic variation* in climate. The periodicity of Milankovitch cycles is due to longer term (22,000 year), regular variations in the Earth's distance from the sun. (B,C,D) In contrast, *discontinuities*, *jumps*, *trends*, or *increasing variability* can all represent different forms of *climate change*. In these cases, the means of climatic variables do not remain stationary within the time domain of interest. (B) After a jump or discontinuity, a new baseline of climate variability emerges that is different from the old. (C) *Trends* in climate refer to changes in which the range of variation of climatic variables remains more or less within historic norms, but there is a movement of the mean in a single direction, consistently greater or consistently less than the historic average. When such consistent, sustained movement occurs, it is appropriate to speak of such variation as *climate change*. (D) *Increasing variability* occurs when the means of climatic variables remain the same, but their range of variation increases. Now individual "weather" events become more unpredictable and less tightly clustered around historic means. (T. R. Karl and K. E. Trenberth, Yale University Press. Copyright 2005 by Yale University.)

refer to changes in which the range of variation remains within historic norms, but with movement of the mean in only one direction, consistently greater or less than the historic average. When such sustained directional movement occurs, such variation is accurately called *climate change*. *Increasing variability* (Figure 5.2D) occurs when the means of climatic variables remain the same, but their range of variation increases. Now individual "weather" events become more unpredictable and less tightly clustered around historic means.

5.1.3. Should Contemporary Global Warming Be Called "Climate Change?"

Perhaps the most obvious characteristic of climate is temperature. On Earth, temperature varies spatially, seasonally, and historically. As an index of energy, the range of temperatures on Earth, both now and in past times, is driven by the absorption of solar radiation from the sun. The net incoming energy from such solar radiation is, as an "Earth average," 342 watts per square meter (W/m^2) (Karl and Trenberth 2005). Over the entire Earth's surface, this energy input is equal to 175 PW (1×10^{15} W). Given that the largest human-constructed power stations have energy production capacities of about 1,000 MW, the incoming energy is approximately equivalent to that which could be produced by 175 million such power stations (Karl and Trenberth 2005). About 31% (107 W/m^2) of this energy is reflected back into space by clouds and atmospheric particles (aerosols) and never reaches the Earth's surface, but the remaining 69% (235 W/m^2) is available to warm both the Earth and its atmosphere (Figure 5.3).

The Earth balances this input by reradiating such energy back to space. However, in the act of being reflected from the Earth's surface, the wavelength of the emitted radiation is changed to long-wave "infrared" radiation. The form of the reflected radiation is important because such wavelengths are absorbed by certain gases in the Earth's atmosphere, notably water vapor (H_2O), methane (CH_4), ozone (O_3), nitrous oxide (N_2O) and carbon dioxide (CO_2). Such absorption creates a net influx of energy to the Earth. To conserve the energy balance of the system, there must be some change in non-radiative energy states of the system, including temperature. This change is known as ***radiative forcing***. The outcome of radiative forcing is that, as a result of such absorption of energy, which is then emitted both up (to higher layers in the atmosphere) and down (toward the surface of the Earth), temperature must rise.

Because of their capacities to absorb long-wave radiation, the gases which do the absorbing are called ***greenhouse gases***. Such absorption warms the Earth, making it a more hospitable place for life than if the influx and outflux of solar radiation to and from the Earth were equal. Without such warming, the average near surface temperature of the Earth

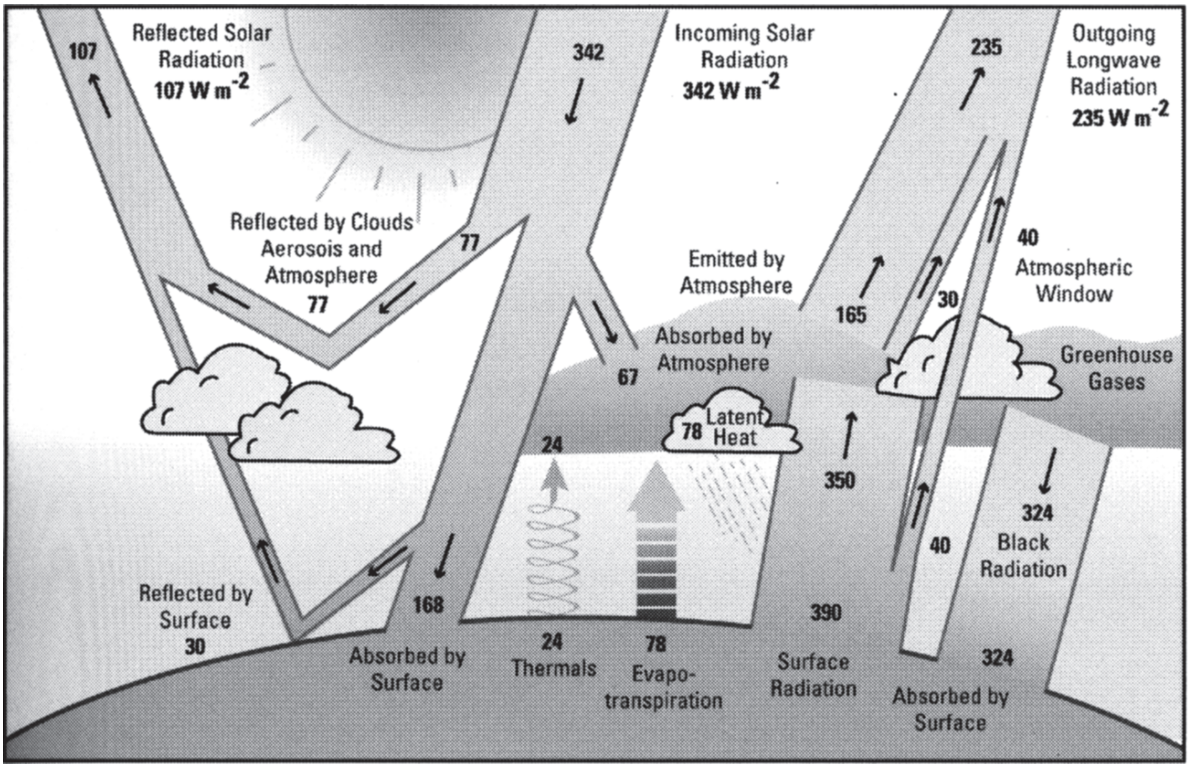

FIGURE 5.3. The radiation budget of the Earth. (T. R. Karl and K. E. Trenberth, Yale University Press. Copyright 2005 by Yale University.)

would be −19°C instead of its current 14°C. Each greenhouse gas differs, not only in its capacity to absorb long-wave radiation, but in other traits that affect its contribution to the overall warming producted. Specifically, the key factors are: (1) the amount of gas released into the atmosphere per year, (2) the length of time that it stays in the atmosphere before being destroyed or removed, (3) any indirect effect it has on atmospheric chemistry, and (4) the concentration of other greenhouse gases. If all of these factors are collectively taken into account, H_2O and CO_2 emerge as the greenhouse gases that contribute most to this warming effect, with water vapor accounting for about 60% of the warming effect and carbon dioxide about 26% (Kiehl and Trenberth 1997). Humans, through various activities, make net additions of greenhouse gases into the atmosphere. Of these, the largest additions are of CO_2 produced through the combustion of fossil fuels. This addition is significant, because, as noted above, CO_2 is, next to water vapor, the gas most responsible for the greenhouse effect. The potential for such additions of CO_2 to increase atmospheric and surface temperatures has been recognized for a long time. The Nobel laureate Swedish chemist Svante Arrhenius was the first scientist to develop a model quantifying the radiation budget of the Earth's atmosphere and surface (Arrhenius 1896), and from this was able to create a climate model that agrees with many aspects of modern climate models (Ramanathan and Vogelmann 1997). Arrhenius was motivated by his desire to understand past temperature variations from the Quartenary Period, but he also applied his results to present conditions, and was the first to predict the consequences of industrial emissions of CO_2 on future climate change, including global warming (Saavedra 2002).

Direct measurements of atmospheric CO_2 concentrations began in 1958 at the Mauna Loa Observatory in Hawaii (USA), but older records of atmospheric CO_2 concentrations can be estimated by indirect indices, especially by measuring the concentration of CO_2 and other greenhouse gases trapped in ice cores, some of which, such as those from Antarctica, can provide a continuous record of such concentrations over the last 450,000 years (Figure 5.4). The molecules of CO_2 trapped in this ice also provide a record of atmospheric temperature inferred through variations in the concentration ratios of different isotopes of oxygen atoms in their molecules. Such examination reveals three key facts. First, atmospheric CO_2 concentrations and temperature show tight correlation. Second, until recently, concentrations of atmospheric CO_2 varied between 280 ppm (warmest periods) and 180 ppm (coldest periods) over the last 450,000 years. Third, current levels of atmospheric CO_2, at 380 ppm, are higher than ever before recorded during this 450,000-year period.

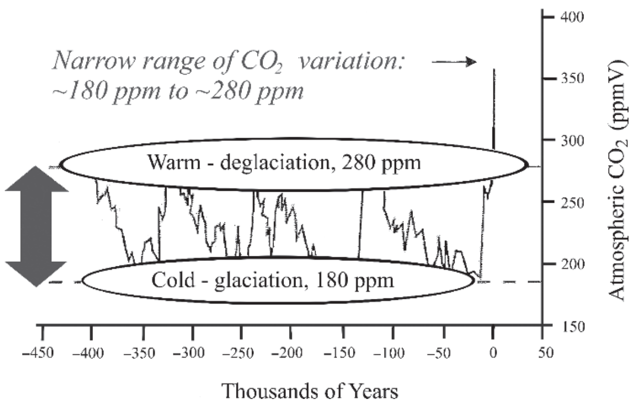

FIGURE 5.4. Temperature and CO_2 concentrations estimated from Antarctic ice cores for the previous 450,000 years. (M. J. Apps, P. Bernier, and J. S. Bhatti. Forests in the global carbon cycle: implications of climate change. In: J. S. Bhatti, R. Lal, M. J. Apps, and M. A. Price (eds) Climate change and managed ecosystems. Copyright 2006 by Taylor & Francis.)

Climatologist M. J. Apps and his colleagues, drawing on ice cores and other inferential data permitting estimates of CO_2 and temperature going back 1.5 million years, noted this tight and highly predictable historical oscillation. Studying these trends, they remarked *Throughout at least the last four glacial cycles, spanning nearly 1.5 million years prior to the 20th century, the atmospheric concentration of* CO_2 *only varied between ~180 ppmv during glaciations, when the global temperature was 8 to −9°C colder than today, and ~280 ppmv during the interglacial periods when the temperature was similar to present values. … This narrow range of variation in atmospheric* CO_2 *is remarkable given that its concentration is determined by a highly dynamic biogeochemical cycle. … This generally tight domain of stability between variations in* CO_2 *and global temperature … suggests that the global carbon cycle has been controlled by powerful biological feedback processes that have maintained the climate in a habitable range. The biosphere appears to play a central role in regulating Earth's climate. …*

5.1.4. The Implications of Rapidly Rising CO_2

As already noted, the current atmospheric concentration of CO_2 of 380 ppmv appears to be higher, by approximately 36%, than any recorded levels of the past 1.5 million years. More troubling is the fact that the current *rate of increase* in atmospheric CO_2 is now five times greater than any known historical increase. As the concentration of atmospheric CO_2 has increased, so has the positive radiative forcing associated with it (Figure 5.5), now at a level 1.5 times what it was in 1800 (Gittay et al. 2002). Just as was seen in the ice cores, global temperatures and atmospheric CO_2 increases have been correlated, such that, from 1901 to 2000, nearly every measured location on Earth, both terrestrial and aquatic, has seen some level of temperature increase (Figure 5.6) (Gittay et al. 2002). Taken as a global average, the Intergovernmental Panel on Climate Change

(IPCC) reported that “the global mean surface temperature has increased 0.6°C (0.4–0.8°C) over the last 100 years, with 1998 being the warmest year and the 1990s *very likely* being the warmest decade” (Gittay et al. 2002). The IPCC uses the phrase “very likely” to indicate a 90–99% certainty. The observed pattern of global temperature increase constitutes a demonstrable *trend* of overall and continually increasing rise in average global temperature, and is therefore correctly described as *climate change*.

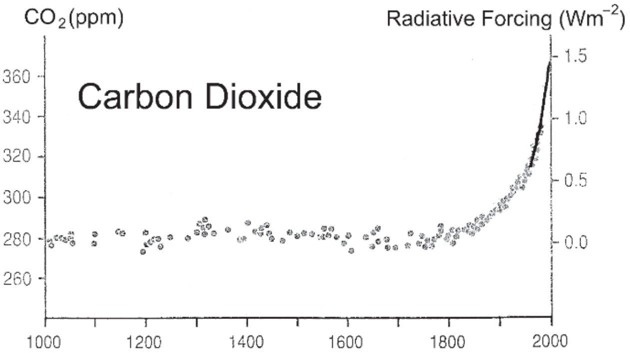

Figure 5.5. Relationship of changes in CO_2 levels and associated radiative forcing in the Earth’s atmosphere over the last 1,000 years. Early sporadic data taken from air trapped in ice (symbols) are consistent with continuous observations and direct measurements since 1958 (solid line). (Technical Paper V, Climate Change and Biodiversity, Intergovernmental Panel on Climate Change, 2002, Courtesy IPCC.)

Carbon moves into and out of the atmosphere in a complex biogeochemical cycle, but one which can be summarized in terms of “sources” and “sinks” and their respective additions or removals (Figure 5.7). Humans add CO_2 to the atmosphere through their combustion of fossil fuels, but they also contribute to net additions through the changes they impose on the landscape. Natural vegetation, and particularly forest vegetation, removes CO_2 from the atmosphere in the process of photosynthesis in which CO_2 is combined with water in the plant to produce glucose according the familiar reaction,

$$6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2.$$

In the complementary reaction of respiration, plants, like animals, also release CO_2 back to the atmosphere, but their overall effect is to remove more CO_2 through photosynthesis than they release through respiration, thus acting as a *carbon sink*. When humans remove forests and other kinds of intact vegetational communities, the net effect is to reduce such carbon removal capacities. Thus, human activity simultaneously adds to carbon sources while reducing the capacities of carbon sinks, resulting in a net increase in atmospheric CO_2.

As an expert witness in testimony before the US Senate’s Energy and Natural Resources Committee, Sir John Houghton, co-chairman of the IPCC, was asked how much of the trend in increasing global temperatures is potentially due to natural variability and how much is due to human activities, Houghton replied carefully and precisely. “In answering the question of how much of the recent warming is due to human activities there are two relevant

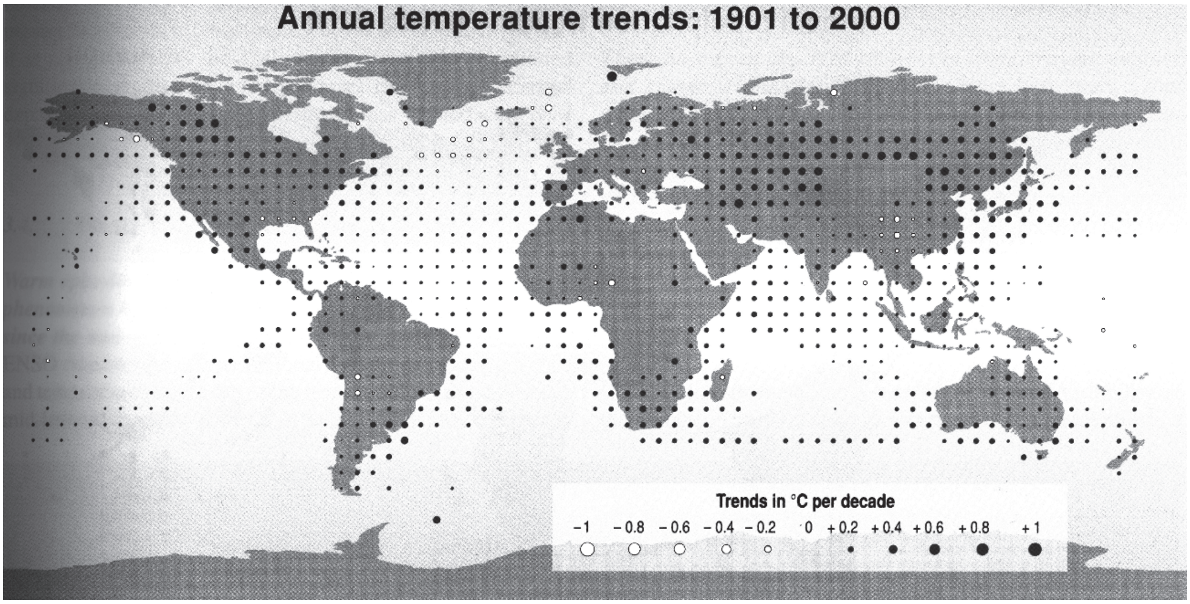

Figure 5.6. Annual global temperature trends from 1901 to 2000. Closed circles indicate temperature increases, open circles temperature decreases. Relative size of symbol indicates magnitude of change. (Technical Paper V, Climate Change and Biodiversity, Intergovernmental Panel on Climate Change, 2002, Courtesy IPCC.)

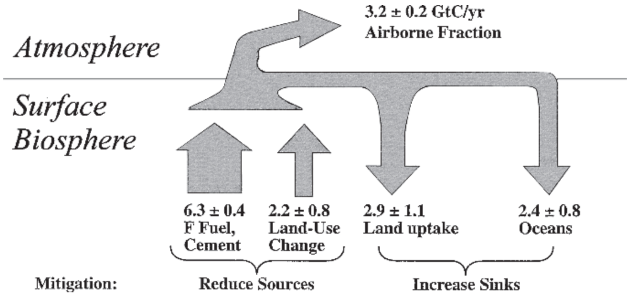

FIGURE 5.7. The global carbon cycle represented in terms of sources and sinks, and the human perturbations to it in the 1990s. Arrow widths depict magnitude of flux. Value for land uptake is inferred as the residual required to balance other fluxes with the observed accumulation (airborne fraction) in the atmosphere. (Data from Houghton 2003. M. J. Apps, P. Bernier, and J. S. Bhatti. Forests in the global carbon cycle: implications of climate change. In: J. S. Bhatti, R. Lal, M. J. Apps, and M. A. Price (eds) Climate change and managed ecosystems. Copyright 2006 by Taylor & Francis.)

considerations: estimates of radiative forcing and estimates of natural variability … by far the largest contribution to radiative forcing over the last 50 years comes from increases in greenhouse gases and … at least 95% of the positive warming force over this period comes from human activities…” (www.net.org/policy/global_warming/pdf/john_houghton_testimony.pdf, 2005, accessed June 2007). Going on to address the issue of natural variability, Houghton noted, after summarizing the major recent studies on this question, that “more than 20% of the rise in global average temperature since 1950 of about 0.45°C is very unlikely (less than 10% probability) to come from unforced variability. Taking these two considerations together leads to the conclusion that it is very likely (greater than 90% probability) that at least 75% of the warming over the last 50 years is due to human activities.” Breaking down the statistical logic, Houghton was reasoning that if 80% of the global temperature increase is outside the range of natural variability, and if 95% of the increase in radiative forcing (the mechanism which causes the unusual increase) is due to human activities affecting CO_2 levels in the atmosphere, then the effective contribution of human activity to such warming is at least 0.8 × 0.95, or 0.76 (76%). Houghton’s estimates of probabilities and percent contributions are not random guesswork. When burned, the CO_2 emitted by fossil fuels possesses a characteristic “signature” of carbon and oxygen isotope ratios that are different from CO_2 originating from other sources. Most additions of CO_2 to our atmosphere bear these signatures. This is one manifestation of what many scientists have come to call the “global fingerprint” of human-induced climate change.

Because overall CO_2 concentrations, and human contributions to them, are still rising, and are expected to continue to rise through at least the first half of the twenty-first century, the world appears to be, at minimum, decades from climate stability. Even the most optimistic scenarios do not foresee a stabilization of CO_2 levels short of 450 ppmv. Even if human-induced CO_2 inputs begin to fall, the persistence time of carbon in the atmosphere and oceans, in a variety of forms, will prevent any significant change in atmospheric CO_2 for decades or centuries. All creatures on Earth must therefore face the reality of coming climate change, one to which they must adapt for the foreseeable future and perhaps until at least the twenty-second century. And for those humans engaged in the work of conserving non-human species, these changes have profound implications. To fully evaluate those implications, we must review one more dimension of the climate change context. Temperature is not the only change in climate change.

5.1.5. Why We Call It “Climate” Change – Non-temperature Variations in Climate in a Warming World

A planet with a greater level of retained radiant energy is one that will experience enhanced rates of evaporation and transpiration, creating, in many parts of the world, more rapid and energetic hydrologic cycles. Thus, in a time of rising global temperatures, precipitation also is more likely to increase in many parts of the world, although historically dry areas may face even more extreme drought conditions. Temperature changes are expected to be non-uniform, with the least change in equatorial regions and the greatest changes in polar areas, resulting, at the poles, in reduced snow and ice cover and reduced areas of sea ice. These effects are now being experienced. Similarly, glaciers on all continents (except Australia, which has no glaciers) are retreating, and attendant glacial and alpine environments are shrinking in size. Water in the oceans is warming. As it does, it increases in volume. This effect, known as thermal expansion, is the main contributor to worldwide sea level rise. Aside from the obvious potential for displacement of human populations on islands and sea coasts, rising sea levels have the potential to destroy up to 20% of the world’s coastal wetland ecosystems. As atmospheric concentrations of CO_2 rise, more CO_2 will diffuse into the oceans, shifting the chemistry of sea water so that its total carbonate alkalinity will decrease (i.e. sea water pH will increase and the oceans will become more acidic). The global “conveyor belt” of ocean currents, which transfers heat energy from tropical areas to colder temperate and polar oceans and their adjacent seacoasts, as well as bringing nutrients up from deeper waters into more productive, photosynthetically active surface waters, will slow, and potentially stop, as the oceans warm (Hoegh-Guldberg 2005). The sum of these and other changes, which are driven by temperature increase but are distinct from it, is why the phenomena we are now experiencing are called “climate change.” The question we now address is, are such changes affecting the biodiversity of the Earth?

5.2. The Global Fingerprint of Climate Change on Biodiversity

5.2.1. Extinction Patterns in Edith's Checkerspot Butterfly

Edith's checkerspot butterfly (*Euphydryas editha*) is a resident species of western North America, ranging from Baja, Mexico northward through most coastal and intermountain states of the US to southwestern Canada. A beautiful and charismatic species, entomologists have long been intrigued by its many phenotypic variations in coloration, wing length, and overall body size. Thus, Edith's checkerspot has a history of record at many sites, some dating back to the nineteenth century. Such data provide the basis for comparing its present distribution to that of its past.

Camille Parmesan, a research scientist at the University of Texas at Austin (USA), made the distribution of Edith's checkerspot an early focus of her research career. Specifically, she was interested in whether this particular species showed any evidence of being affected by climate change. Armed with both present and past records of its distribution from common locations throughout its range, Parmesan was able to evaluate changes in its distribution that were manifested by the changes in the presence or absence (presumed extirpation) of populations at specific sites (Figure 5.8). Upon analysis of the observed pattern, Parmesan concluded, "the actual pattern of extinctions in E. editha was quite simple: population extinctions were four times as high along the southern range boundary (in Baja, Mexico) than along the northern range boundary (in Canada), and nearly three times as high at lower elevations (below 8,000 feet) than at higher elevations (from 8,000 to 12,500 feet).… In concert with global warming predictions, this extinction process had effectively shifted the range of E. editha both northward and upward in elevation since the late 1800s" (Parmesan 2005a:57).

Noting how the elevational shift in this butterfly's range "broke out" at 2,440 m, Parmesan observed,

"This breakpoint correlates with that for changes in snowpack depth and timing of snowmelt across the Sierra Nevada mountains [California, U.S.A.]. Below 2,440 m, snowpack had become 14 percent lighter and melt date had advanced by one week during the twentieth century ($P < 0.05$ for both). In contrast, snowpack had become 8 percent heavier and melt date had not changed above 2,440 m…" (Parmesan 2005a:59).

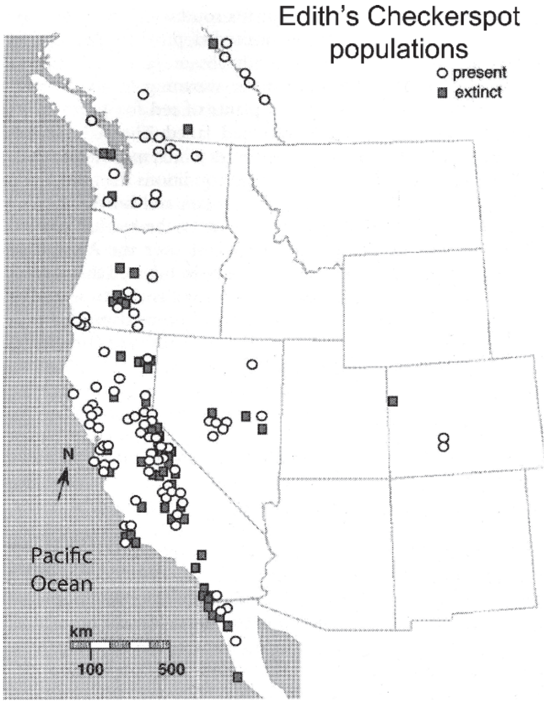

FIGURE 5.8. Patterns of extinctions within the geographic range of Edith's checkerspot butterfly (*Euphydryas editha*), a resident of western North America ranging from Baja, Mexico northward through southwestern Canada. Edith's checkerspot has shown a pattern of extinctions in its southern populations and expansion in its northern populations that fits a response predicted by climate change. (C. Parmesan, Yale University Press. Copyright 2005 by Yale University.)

5.2.2. Finding the Global Fingerprint of Climate Change

Parmesan was intrigued by the results of this initial study of the effects of climate change in a single species. With her colleague, Gary Yohe, of Wesleyan University, she undertook a meta-analysis of published studies evaluating over 1,700 species (Table 5.1) to determine if recent biological trends in range shifts and biological timing events matched climate change predictions. Among these studies, 87% of those studying timing (phenological) events, 75–81% of those examining range boundaries, and 81% of those measuring community abundance documented changes consistent with predictions of climate change. Overall, Parmesan and Yohe documented poleward range shifts of 6.1 km per decade and advancement of spring events by 2.3 days per decade in these studies (Table 5.1). These changes were not random, but consistently in the direction expected from climate change. They represent a "diagnostic fingerprint" of the impact of global climate change on biodiversity. "We define a diagnostic fingerprint," wrote Parmesan and Yohe, "of temporal and spatial 'sign-switching' responses uniquely predicted by twentieth-century climate trends. Among appropriate long-term/large-scale/multi-species data sets, this diagnostic fingerprint was found for 279 species. This suite of analyses generates 'very high confidence' (as laid down by the IPCC) that climate change is already affecting living systems" (Parmesan and Yohe 2003:37).

TABLE 5.1. Summary of biological change events from a meta-analysis of studies of 1,700 species showing change in timing of biological events (phenology) or changes in distribution or abundance in relation to changes predicted by climate change theory.

Type of Change	Changed as Predicted	Changed Opposite to Prediction	*P*-value
Phenological ($N = 484/(678)$)	87% ($n = 423$)	13% ($n = 61$)	$<0.1\times10^{-12}$
Distributional changes			
At poleward/upper range boundaries	81%	19% –	
At equatorial/lower range boundaries	75%	25% –	
Community (abundance) changes			
Cold-adapted species	74%	26% –	
Warm-adapted species	91%	9% –	
$N = 460/(920)$	81% ($n = 372$)	19% ($n = 88$)	$<0.1\times10^{-12}$
Meta-analyses			
Range-boundaries ($N = 99$)	6.1 km m^{-1} per decade northward/upward shift[a]		0.013
Phenologies ($N = 172$)	2.3 days per decade advancement[a]		<0.05

[a] Bootstrap 95% confidence limits for mean range boundary changes are 1.26, 10.87; for mean phenological shift the limits are –1.74, –3.23.

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More troubling than absolute changes in biological events is the growing amount of evidence that such changes in an individual species might disrupt the coordination of activities between this species and other species in any number of interactions, such as predator and prey, parasite and host, or pollinator and flower. Visser and Both reviewed the ecological literature for evidence of just such disruptions in 2005, but, at that time, few published studies had investigated this potential problem. Nevertheless, of 11 studies that did specifically examine the coordinated timing of biological events, 8 demonstrated that the species affected by climate change was more out of synchrony now that at the start of the study, and in most of these cases, negative fitness consequences of such disruption were directly observed or predicted (Visser and Both 2005). For example, Inouye and his co-workers at the Rocky Mountain Biological Laboratory in Colorado, USA found that, from 1976 to 1999, yellow-bellied marmots (*Marmota flaviventris*), large ground squirrels that live mainly in montane environments of the western United States, had advanced their emergence date by 38 days as a result of warmer local spring air temperatures. Such advancement has put them out of synchrony with most of the surrounding plant species, their major food source. At the same study site, American robins (*Turdus migratorius*) had advanced their arrival dates over about the same period (1974–1999) by 14 days, and this increasingly early return spread the difference between their arrival and the average first appearance of bare ground (which robins require for foraging) by an additional 18 days (Inouye et al. 2000). Of even more importance biologically are the coordinated relationships between many species of butterflies and the particular plant species they select as hosts for their larvae (caterpillars). This relationship is critical if the larvae are to have sufficient food to develop into adult butterflies. Many studies have shown that when sufficient asynchrony occurs in this relationship, the butterfly population crashes and extinction results. Not surprisingly, the recorded asynchronies and consequent extinctions are not random. They predominate in drought and, for mountain butterflies, low snowpack years (reviewed in Parmesan 2006), and they are highly skewed in both latitude and elevation. Extinction events have predominated in lower latitude and elevation populations, shifting the range of extant populations northward and upward (Parmesan 1996, 2003, 2005b).

5.2.3. Can Climate Change Cause Extinction of Local Populations?

5.2.3.1. Climate Change and Pikas

The pika is a small, guinea pig-sized North American lagomorph that lives at high elevations in loose rock (talus) on steep slopes, often associated with alpine plant communities. Pikas survive the long, harsh winters of their high elevation, alpine environments by, in part, working extra hard during the short alpine growing season, usually from late June or early July to late August or early September. During this season, adult pikas cut (actually, bite) down and then dry various kinds of herbaceous grasses and forbs which, after drying, they store in their below-ground burrows, providing a supply of food in harsher seasons. Recall that pikas were one of several species that zoologist Joseph Grinnell studied in the early twentieth century to demonstrate the role of temperature in determining species' ranges (Grinnell 1917). In fact, Grinnell persuasively used temperature to explain why pikas could be found at much lower elevations on the north slopes of California's Sierra Mountains than they could in the very same mountains on south slopes, which experienced higher temperatures at the same elevations (Grinnell 1917:122). A pika's overwinter survival depends on storing sufficient forage during the summer months. Pikas forage vigorously during summer, but are sensitive to heat when doing it. They sometimes stop foraging in August, when temperatures are highest, at low elevation sites and die if exposed to temperatures greater than 31°C (88°F) for more than 30 minutes (Smith 1974).

Considering the full range of elevations at which pikas are known to occur, Erik Beever of the University of Nevada – Reno (USA) and his colleagues, Peter Brussard and Joel Burger, surveyed, from 1994 to 1999, sites of 25 historic pika populations in the Great Basin of Nevada and other states that had been known since the 1930s (Beever et al. 2003). Among these 25 populations, 7 had experienced recent extinctions, all at significantly lower elevations than the surviving 18. Human disturbance, which was minimal at all sites, was not the culprit. Although climate change could not, in this study, be definitively proven as cause of extinction, the pattern of extinction seen in these pika populations was consistent with a pattern predicted by climate change.

5.2.3.2. Climate Change and Desert Bighorn Sheep

Beever et al.'s pika study raises suspicions of climate change as the culprit of these pika extinctions, but does not prove cause and effect. A more direct investigation of the role of climate change in extinction was undertaken by Clinton Epps and his colleagues in California on the desert bighorn sheep (*Ovis canadensis nelsoni*), a subspecies of the more widespread Rocky Mountain bighorn sheep (*Ovis canadensis*). If any creature was ever pre-adapted to global warming, it is the desert bighorn. This subspecies has persisted even, as Epps and his colleagues noted, "… as the climate of the southwestern United States has become increasingly arid since the end of the Wisconsin glacial period…" (Epps et al. 2004:103). But past hardships may be nothing compared with those to come. Desert bighorn exist as a metapopulation of widely scattered subunits in generally isolated mountain ranges with desert or semidesert landscapes in between. The persistence of individual metapopulation subunits is variable. The question Epps et al. posed is, are differences in persistence related to differences in climate and do overall patterns of persistence fit the predictions of regional climate change?

From 1901 to 1987, mean annual temperature in the deserts of the southwestern United States has increased 0.12°C per decade (Lane et al. 1994), while, at the same time, annual precipitation has decreased by roughly 20% over the last century in southeastern California (Ball et al. 1998). Drought can cause increased mortality among desert bighorn sheep (Monson 1960) and affect recruitment dynamics (Wehausen et al. 1987). Epps and his colleagues used simple presence and absence data to examine the effects of climate and other factors in determining metapopulation structure. They first examined all mountain sheep ranges known to hold or to have held desert bighorn populations in California, and then scored these for variables that described climate, metapopulation dynamics, human impacts, and other environmental factors. Climate factors such as temperature and moisture affect annual nutrient availability in forage plants used by bighorns. However, Epps et al. used elevation as a surrogate variable for temperature because, in this environment, the two are strongly correlated, and elevation can be measured much more precisely at individual sites used by bighorns than can temperature.

Classic ***metapopulation theory*** predicts that extinction probability should decrease with increasing area of habitat patches available for population subunits (Hanski 1991, 1997) and with increasing immigration of individuals from one population subunit to another, which in turn, depends on interpatch distance. With these traditional assumptions in mind, Epps et al. tested two hypotheses to determine if extinctions were linked more strongly to the processes of metapopulation dynamics than to overriding climate conditions. Based on the previously stated predictions, Epps et al.'s first hypothesis was that extinct populations inhabit ranges with smaller two-dimensional area than ranges with extant populations. Using similar reasoning, the second hypothesis was that extinct populations are more isolated from other mountain ranges containing bighorn sheep than are extant populations. (Epps et al. 2004). Thus, these investigators also measured the size of the area used by each population subunit ("patch size") and its relative isolation from other subunits (mean distance to other subunits), along with parameters related to geology (which affects both vegetation and water availability) and various aspects of potential human disturbance (Table 5.2). All parameters were then incorporated in logistic-regression models that evaluated the strength of each parameter in correctly predicting population persistence.

In the models that resulted, all parameters that were climate-related or climate-dependent (elevation, precipitation, and the presence of dependable springs) were strongly correlated with population persistence. Bighorn populations that inhabited lower, drier mountain ranges were more likely to go extinct (Figure 5.9). The best predictive models contained the parameters of maximum average annual precipitation, maximum elevation, presence of domestic sheep grazing allotments, and the presence of dependable springs. Extinction was, in the words of Epps and his colleagues, "negatively correlated with precipitation, elevation, and dependable springs, but positively correlated with the presence of domestic-sheep grazing allotments" (Epps et al. 2004:108). In other words, for a given population, the more precipitation, the greater the elevation, and the more dependable springs present, the lower the probability of extinction. But the greater the presence of domestic sheep, the greater the probability of extinction.

Recognizing the implications of these findings in terms of ongoing and projected future climate changes in this region, Epps et al. wrote, "… in the maximum

TABLE 5.2. Parameters included in logistic-regression analyses of extinctions of desert bighorn sheep (*Ovis canadensis nelsoni*) populations in California, USA.

Parameter	Descriptive Statistic
Precipitation	Maximum value in each population polygon
Elevation	Maximum
Dependable springs	Presence/absence
Granite	Area (%)
Volcanic rock	Area (%)
Limestone	Presence or absence
Isolation	Harmonic mean of distance to nearest three populations
Area	Polygon area
Distance to towns/cities	Minimum distance from sheep polygons
Mining	Presence or absence of "economically viable mineral deposits"
Road access (ordinal)	Closed (1), approved roads (2), existing roads (3)
Feral burros and horses	Presence or absence
Cattle	Presence or absence of grazing allotments
Domestic sheep	Presence or absence of grazing allotments

Source: Epps et al. (2004). Effects of climate change on population persistence of desert-dwelling mountain sheep in California. *Conservation Biology.* Copyright 2004 by Blackwell Publishing.

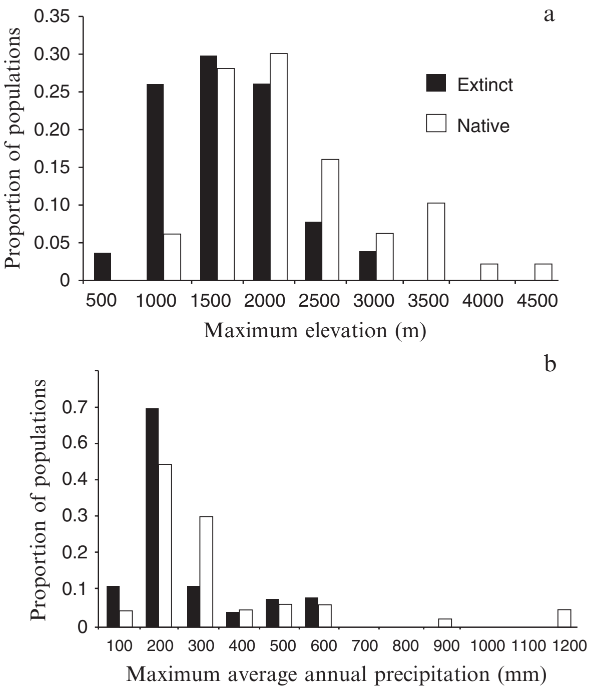

FIGURE 5.9. Distribution of extinct and extant populations of desert bighorn sheep (*Ovis canadensis nelsoni*) in relation to (a) maximum elevation (m) and (b) maximum average annual precipitation (mm) values associated with the range of each population. Extinct populations are more prevalent on lower, drier ranges. (Epps et al. (2004). Effects of climate change on population persistence of desert-dwelling mountain sheep in California. *Conservation Biology.* Copyright 2004 by Blackwell Publishing.)

temperature-change scenario of +2.0°C in the next 60 years, average risk of extinction increased substantially to 0.26. Extinction risk also increased drastically when precipitation was reduced, such that a 0.7°C increase combined with a 12% decrease in precipitation elevated extinction probabilities to levels observed with a 2.0°C increase with no change in precipitation. Average extinction risk increased from 0.21 (no change) to 0.30 when a 2.0°C increase was combined with a 12% precipitation decrease" (Epps et al. 2004:108–109). Further, "Populations in mountain ranges of lower elevation were much more likely to become extinct, particularly at <1,500 m (Figure 5.9a). Populations in regions with the lowest annual precipitation, especially <200 mm annual precipitation, were also more likely to become extinct (Figure 5.9b), as were populations without dependable springs and populations in which domestic-sheep grazing allotments formerly overlapped or abutted desert bighorn habitat. This suggests not only that desert bighorn sheep are vulnerable to climate warming but that climate warming has already affected their distribution in California" (Epps et al. 2004:109).

Recall that Epps and his colleagues had hypothesized, based on predictions of metapopulation theory, that population subunits using smaller areas and that were more isolated from one another should be more prone to extinction. This was not the case. Population extinction was not sensitive to patch size (two-dimensional area of the inhabited mountain ranges) or to the degree of population isolation. But why, exactly, was a climate effect able to override a fundamental population process that has been demonstrated to be such a strong influence on metapopulation persistence in other studies? Epps et al. give this explanation, "The strong effect of patch size on persistence is thought to result from the expected correlation with population size if populations are strongly regulated by density dependence. If populations are regulated by environmental factors, however, one can expect a much weaker relationship between patch size and population size.… Our findings that precipitation and elevation, but not patch size, were correlated with population extinction are consistent with strong environmental regulation of desert bighorn sheep populations" (Epps et al. 2004:110).

5.3. Climate Change in Ecosystems – Species Loss and System Degradation

5.3.1. Climate Change at Ecosystem Levels: Biome Boundaries and Elevational Shifts

The work of Beever et al. and Epps et al. provide warrant for concern that climate changes can cause extinction of local populations. However, the ultimate goal of conservation biology is not to document extinction, but to prevent it.

A focus on extinction prevention means that conservation biologists must understand how climate change is likely to affect their targeted species and habitats, and plan accordingly to mitigate negative impacts. As bioclimatologists Lee Hannah and Laura Hansen point out, "Climate change affects selection of [conservation] targets in two fundamental ways. First, it will alter ecoregion boundaries … [resulting] in different biome boundaries in the future, which may change the size or configuration of an ecoregion.… The second way in which climate change can affect target selection is by exacerbating existing threats.… Therefore, climate change is likely to increase the number of conservation targets, through both changing the planning area and by increasing the number of species at threat" (Hannah and Hansen 2005:331).

Conservation biologist Reed Noss, commenting on the prospect of conservation management under the stress of climate change, noted, "The challenge for conservationists is not to prevent change. It is to keep rates, scales, and intensities of change in ecosystems within the historic range of variability for those systems – or, at least, to come close. Conservationists must also develop strategies to mitigate the effects of inevitable changes that fall outside the historic range of variability" (Noss 2001:580). But what sorts of strategies can mitigate the effects of climate change? We begin to explore the answer to that question by first defining climate change relative to ecological boundaries, starting with a study of how climate change affects elevational life zones.

5.3.2. Life Zone Changes in Tropical Forests

Worldwide, many forests occur in mountainous regions. Therefore, the effects of climate on forests are often most profoundly manifested in elevational effects rather than latitudinal ones. C. A. Enquist examined the effect of climate change on forest elevational life zones ("Holdridge Life Zones") in Costa Rica, estimating the species richness and number of endemic species in every Holdridge Life Zone by direct field measurements.

Of all the available types of ecosystem classification, Holdridge Life Zones are uniquely suited to evaluations of climate change on ecosystems. The Holdridge Life Zone system includes 38 life zone categories defined by plant moisture demand and ***biotemperature***. Biotemperature, in this classification system, is defined as the mean value of daily temperature above 0°C divided by 365. Thus, as Peterson et al. put it, "Biotemperature, which is closely related to growing degree days, gives a measure of the heat available during the growing season and is likely to be more directly related to plant growth than is mean annual temperature" (Peterson et al. 2005:219).

Using current and projected levels of temperature and precipitation from different climate models and Holdridge life zone criteria, Enquist predicted how such zones would change elevationally under different climate scenarios, and how this might affect species richness and numbers of endemic species in each zone. He noted that "High elevation life zones were shown to be more sensitive to changes in temperature, while lower elevation life zones tended to be more sensitive to changes in precipitation. Regional life zone diversity was greatly reduced in an extreme wet and warm climate scenario. Three elevation-associated life zones (lower montane rain forest, montane rain forest, and premontane rain forest) ranked in the top four in percentage number of endemic species. The lowland seasonally dry forest life zone ranked second in this group, suggesting that this life zone has a unique species composition in comparison with other lowland Holdridge life zones. Of the nineteen life zones, these four life zones displayed particular sensitivity to the climate changes modeled here" (Enquist 2002:519).

5.3.3. Elevational Shifts in Tropical Cloud Forests: The Case of the Golden Toad

The kinds of changes that Enquist modeled in general categorical terms can have very specific effects on particular life zones. It appears that some of the ecosystems associated with such zones, and their endemic species, cannot be saved by mitigation against climatic effects. The most sensitive of these may be the Central American cloud forests. Cloud forests, such as those in Costa Rica, are distinctive not only in the amount of rainfall they receive, but in the historically "misty" environment that predominates in them. Usually found at the upper elevations of high tropical mountains, it was historically rare for such systems to experience consecutive mist free days. Amphibians, the one class of vertebrates that depends on direct respiration through their skin as much as on gills or lungs, must keep their skin moist in order for such respiration to occur. Cloud forests provide an environment of relatively constant high humidity that could be uniquely beneficial to amphibians through its enhancement of this respiration pathway. Amphibian richness in cloud forests has historically been large, and contained such charismatic endemic amphibians as the golden toad (*Bufo periglenes*) (Figure 5.10) among others.

Alan Pounds and his colleagues, who have long studied cloud forests amphibians, report changes they have seen over decades of field work and describe mechanisms through which climate change alters species composition. Based on direct measurements, they noted, "Dry days have increased in frequency since the 1970s and have increasingly coalesced into dry periods. Whereas mist free periods in the 1970s rarely exceeded two days, they have recently lasted up to three weeks" (Pounds et al. 2005:71) (Figure 5.11). The outcomes of such changes were predictable.

FIGURE 5.10. The golden toad (*Bufo periglenes*), a species endemic to tropical cloud forests and their environments of high humidity. Under increasingly dry conditions in these forests, the golden toad has disappeared from the wild. (Photo courtesy of Andrew Jackson. Copyright Michael and Patricia Fogden. Used by permission.)

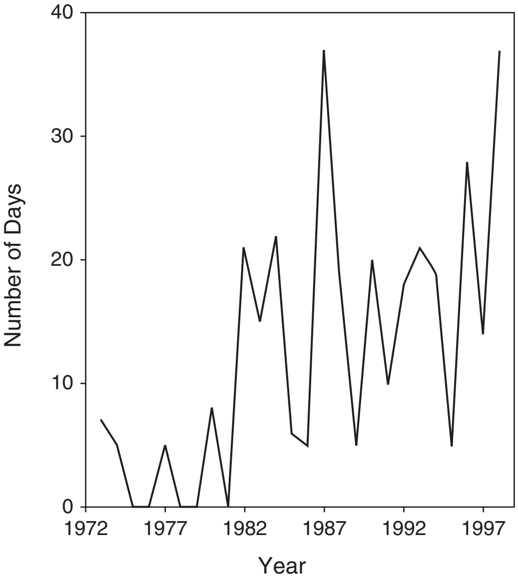

FIGURE 5.11. Trends and fluctuations in the number of dry days in a tropical cloud forest in Costa Rica's Monteverde Cloud Forest. *y*-axis values represent numbers of dry days (days with no measurable precipitation) forming periods of 5 or more consecutive dry days during the dry season. Note the trend over time toward more and more dry day periods. (J. A. Pounds, M. P. L. Fogden, and K. L. Masters, Yale University Press. Copyright 2005 by Yale University.)

"Massive declines of frogs and toads were apparent by 1990. A multispecies population crash in 1987 led to the disappearance of the endemic golden toad (*Bufo periglenes*) and many other species.… Twenty of the 50 were missing throughout the surveys of a 30-km^2 area during 1990–1994, and there is still little sign of recovery 15 years after this crash" (Pounds et al. 2005:70–71).

Pounds et al. evaluated the probability that such disappearances might be random events. Summarizing their analysis, they noted, "Tests of null models based on long-term studies of other amphibian assemblages suggest that the number of disappearances is improbable in the context of normal demographic variability. Moreover, surviving populations for which baseline data exist have fluctuated far below crash levels, undergoing simultaneous downturns in 1994 and again in 1998" (Pounds et al. 2005:71).

As the humidity of cloud forests declined, other species of amphibians and other animals, traditionally found on lower slopes, colonized higher elevations. But the cloud forests could go no higher. As Noss concluded, summarizing other studies, "Simulations of changes in temperature and moisture under doubled CO_2 show an upward shift in the cloud layer of hundreds of meters during the winter dry season, coupled with increased evapotranspiration.… Cloud forests have nowhere to shift and are expected to be lost, along with their endemic species … meanwhile, species from lower elevations have invaded these forests. … In situations such as these, ex situ preservation of species in zoos and botanical gardens until global warming is reversed may be the only way to avoid extinction" (Noss 2001:586).

Although the effects of climate change can be devastating to individual species, they are often synergistic, affecting multiple species interactions and ecological processes such as those of predator and prey and parasite and host. One example of such synergism is found in the effects of climate change on one species of tree, the whitebark pine (*Pinus albicaulis*) and its ecological interactions with other species.

5.4. Climate-Mediated Mechanisms of Ecosystem Change

5.4.1. Climate Influences on a Keystone Species: The Case of the Whitebark Pine

The whitebark pine is a conifer of the western United States and Canada (Figure 5.12) adapted to conditions at high elevations. In fact, if one hikes up the slope of a typical western North American mountain range, such as the Rockies, whitebark pine will be the last tree species present before one reaches the treeless alpine vegetation and talus slopes of the high plateaus and peaks. Whitebark pine produces a heavy, nutritious, and tasty seed ("nut"), with highly variable seed production in different years. Because of the high mass of the seed, it has, on its own, very limited dispersal ability. However, because of the pine's mutualistic relationship with a bird, the Clark's nutcracker (*Nucifraga columbiana*), the seed is spread great

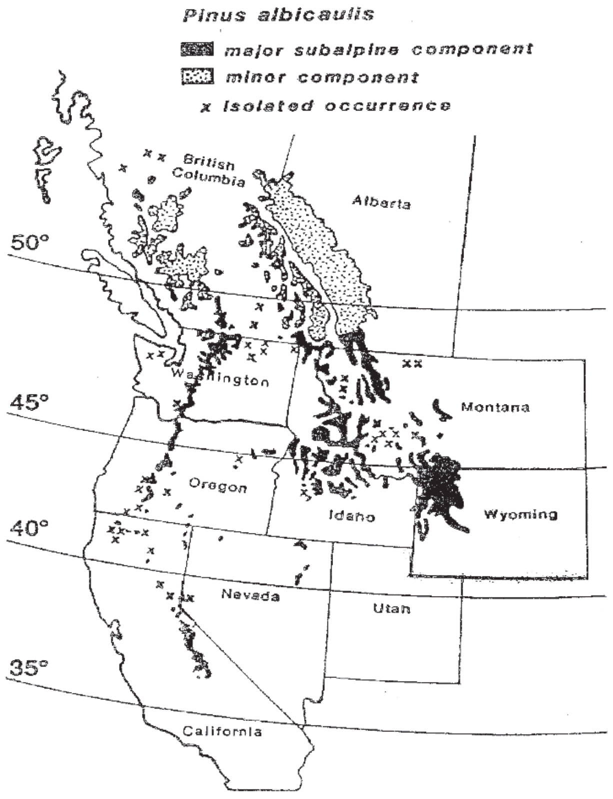

FIGURE 5.12. Range map of the whitebark pine (*Pinus albicaulis*), a western North American conifer that serves as an important food source for animal species such as Clark's nutcracker (*Nucifraga columbiana*) and grizzly bear (*Ursus arctos horribilis*), but whose recently declining range may be related to climate change conditions that increase its susceptibility to fire, adverse effects of competition, and disease. (From *Wildlife Responses to Climate Change: North American Studies* by S. H. Schnieder and T. L. Root, eds. Copyright 2002 by Island Press. Reproduced by permission of Island Press, Washington, DC.)

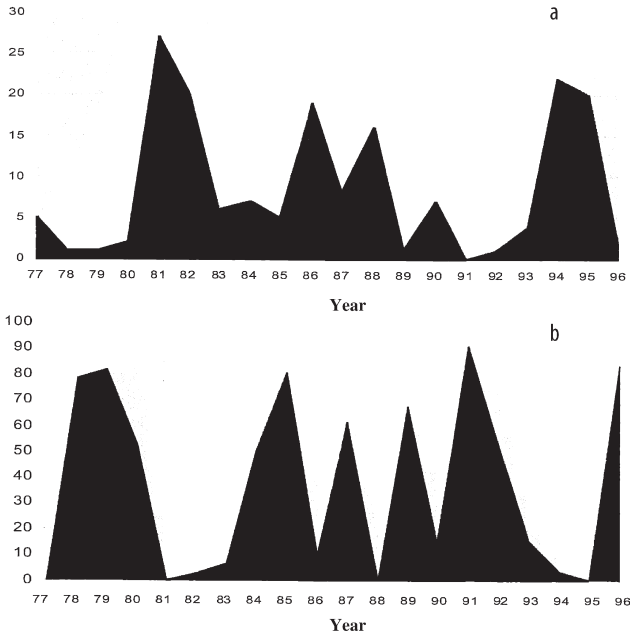

FIGURE 5.13. Annual number of management trappings (a) of grizzly bears in the Greater Yellowstone Ecosystem (GYE), U.S.A. from 1977 to 1996 concurrent with percent of whitebark pine seeds in grizzly bear scat during the same years (b). In years when seeds are unavailable as a major food source (low production years), trappings increase as bears range more widely in search of alternative food, and suffer greater mortality from human contact. (From Koteen 2002. Figure courtesy of David J. Mattson, US Geological Survey, Biological Resources Division.)

distances throughout the mountains. Clark's nutcrackers, which prefer habitat near the upper edge of the tree line, not only use the seeds of the whitebark pine as a short term food source, but also "plant" the seeds in caches over many miles of landscape. Direct estimates indicate that a single Clark's nutcracker may plant 50,000–120,000 seeds in up to 8,000 caches (Koteen 2002:346). It is the diligence of the bird, not the dispersal ability of the seed, to which the whitebark pine probably owes its extensive distribution throughout western North America.

Another species feeding on whitebark pine nuts is the grizzly bear (*Ursus arctos horribilis*), a subspecies of brown bear, once widespread in North America but now confined mainly to the northwestern portions of Montana and Wyoming, the latter population living in Yellowstone National Park and its surrounding national forests, the "Greater Yellowstone Ecosystem" (GYE). Grizzlies obtain from 25% to 67% of their caloric energy from whitebark pine seeds, depending on the availability of the crop (Mattson et al. 2001). In years of high mast production by the whitebark pine, grizzlies remain close to productive stands of whitebark pine and greatly reduce their movements. In years of poor mast production, they wander more widely in search of food. These wanderings result in a greater need for and higher numbers of management trappings to remove grizzlies from situations of bear-human conflicts (Figure 5.13), with higher rates of bear mortality associated with their encounters with humans (Mattson et al. 2001).

Although historically widespread in this region, recent decades have seen a gradual but persistent recession of the range of the whitebark pine, up to 90% range reduction in some areas. Various environmental stressors have contributed to such recession, but one of the most important is a pathogen. The whitebark pine is vulnerable to a particular disease organism, the white pine blister rust. The blister rust, a type of fungus, spreads to the whitebark pine through an intermediate host, the gooseberry or currant (*Ribes* spp.) (Figure 5.14). Although *Ribes* was historically uncommon at the high elevations used by whitebark pine, warming temperatures and

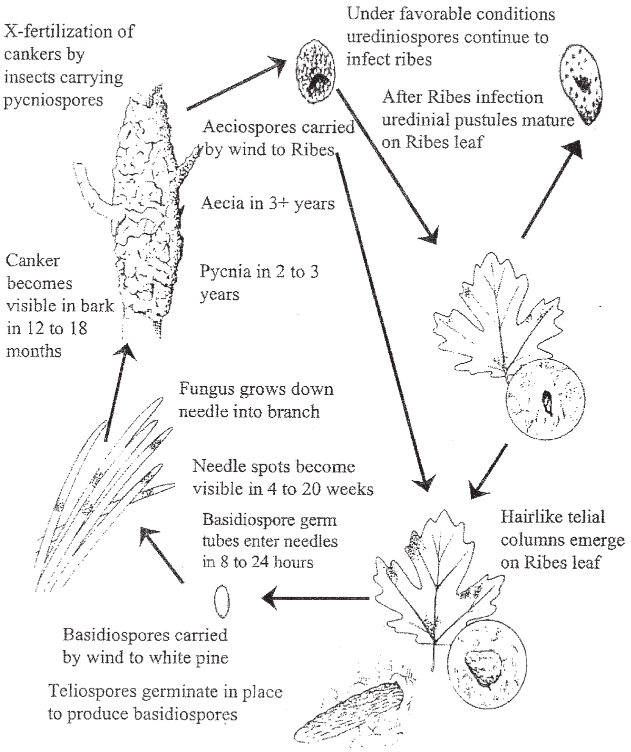

FIGURE 5.14. Life cycle of the white pine blister rust, a type of fungus, that can spread to the whitebark pine through an intermediate host, the gooseberry or currant (*Ribes*). Although *Ribes* was historically uncommon at the high elevations used by whitebark pine, warming temperatures and increasing precipitation in recent decades are increasing overlap between the species and increasing the prevalence of conditions favorable for infection in whitebark pine. (From *Wildlife Responses to Climate Change: North American Studies* by S. H. Schnieder and T. L. Root, eds. Copyright 2002 by Island Press. Reproduced by permission of Island Press, Washington, DC.)

increasing precipitation in recent decades are increasing overlap between the species and increasing incidence of infection in whitebark pine, especially since the fungus can spread more readily under moist conditions. Whitebark pine, being the conifer adapted to the highest elevations, cannot "shift up" like lower elevation species as the climate warms. Lodgepole pine (*Pinus contorta*), the species historically occupying elevational zones immediately below the whitebark pine, has moved upward in elevation in response to climate warming. As the distribution of whitebark pine and lodgepole pine have increasingly overlapped, lodgepole pine has proven the superior competitor, demonstrating an ability to displace whitebark pine over time where the two species become established on the same site. In addition, warming trends now occurring in the whitebark pine's range make the landscape more vulnerable to fire, a disturbance to which the whitebark pine is poorly adapted, but one to which lodgepole pine is favorably adapted.

Investigating the implications of climate change in the complex ecological interactions surrounding the whitebark pine, Laura Koteen developed a climate model for whitebark pine susceptibility to blister rust infestation by first determining regional trends in climate (temperature and moisture) from long-term weather station data in the GYE, and then relating them to conditions needed for optimal transmission of the blister rust. Once the baseline model was constructed and validated from actual data, she iterated it under three projected scenarios of climate change. Because the spread of blister rust is affected primarily by moisture, the scenarios were changed in precipitation, not temperature, with increased precipitation considered likely in future years of projected regional climate change. The scenarios were: (1) 25% increase in interannual variability of monthly precipitation; (2) same as (1) plus 25% overall increase in precipitation, but with the number of precipitation days per month constant; and (3) a 25% increase in mean monthly precipitation by increasing the frequency of precipitation days. Each simulation was run for 50 years using data from four local weather stations. The number of years in which precipitation conditions permitted completion of the blister rust life cycle and transmission to whitebark pine ("blister rust years") was determined at each weather station, as well as the number of "blister rust events" (the number of favorable periods for transmission for blister rust) within each year.

The projected incidence of blister rust increased at all four stations under Scenario 3, at three stations under Scenario 2 and at two of four stations in Scenario 1 (Table 5.3). At one location (Hebgen Dam), the index of blister rust events increased from 150% to 303% in all scenarios. Although effect varied by location and scenario, Koteen's model suggested that, in a warmer and wetter climate, whitebark pine could potentially be greatly reduced or even eliminated at some locations where local effects of climate change favor increased transmission of the blister rust fungus. Should climate change make these more regional in scope, whitebark pine could be reduced over large areas, limiting an important food source for the Clark's nutcracker, grizzly bear, and other species.

TABLE 5.3. Changes in "blister rust index values" under three climate scenarios at four locations of known meteorological conditions in the Greater Yellowstone Ecosystem, USA. Scenarios described in text.

Station	Scenario 1 (%)	Scenario 2 (%)	Scenario 3 (%)
Snake River	94	211	72
Hebgen Dam	150	303	238
Lake Yellowstone	−35	15	18
Gros Ventre Summit	−16	−7	18

Source: From *Wildlife Responses to Climate Change: North American Studies* by S. H. Schnieder and T. L. Root, eds. Copyright 2002 by Island Press. Reproduced by permission of Island Press, Washington, DC.

5.4.2. Climate Influences on Ecosystem Processes: Invasive Species in a Warmer World

The negative effects of climate change can create synergistic interactions with other threats to biodiversity. In one sense, climate change is a special form of habitat loss, since increased temperatures and changes in precipitation may render once optimum habitat unlivable for species with narrow environmental tolerances. Of course, climate change will, for some species, create new or additional habitat. But for others, losses will not be compensatory. Climate change also will change interactions among species. The problem of invasive species, currently one of the greatest threats to biodiversity on Earth, may be amplified by climate change if such changes favor invaders.

Jeffrey Dukes and Harold Mooney, two biologists who are experts on invasive species, assessed the impacts of climate on this problem in these words. "We expect most aspects of global change to favor invasive alien species and thus to exacerbate the impacts of invasions on ecosystems.… These impacts include competitive effects, whereby an invading species reduces resources available to other species, and ecosystem effects, whereby an invader alters fundamental properties of the ecosystem. Either type of effect can threaten native biodiversity, and some ecosystem effects feed back to elements of global change" (Dukes and Mooney 1999:135) (Table 5.4).

Every invasive species presents a unique case history of mechanisms through which the invader becomes established and negatively affects native species. But Dukes and Mooney believe their prediction is warranted in general terms because most invasive species share certain life history traits, traits that confer upon them increasing advantages under a regime of rapid climate change. First, among plants, many invasive species respond positively to elevated CO_2 levels, such as cheatgrass (*Bromus tectorum*), kudzu (*Pueria lobata*), and Japanese honeysuckle (*Lonicera japonica*). As a consequence of elevated CO_2 levels, most plants, including a number of invasive species, use water more efficiently and reduce their rate of transpiration. In areas where plant species abundance is limited by water availability, species that can use water more efficiently will gain a competitive advantage. It is also characteristic of many invasive species that they possess wider environmental tolerances and thus occur over wide latitudinal gradients, preadapting them to climate change. Many invasive species possess high rates of effective dispersal, as well as potential for rapid reproduction and population growth, contributing to more rapid adaptive responses. Species that are able to shift ranges quickly would be at an advantage. As Dukes and Mooney note, "Rapid dispersal is characteristic of many biological invaders. Within the genus *Pinus*, species that are invasive tend to have traits that facilitate rapid range shifting, such as short juvenile period and low seed mass (which is associated with long-distance wind dispersal) …" (Dukes and Mooney 1999:137). Overall, "A rapid anthropogenic climate change might disadvantage species that cannot quickly extend their ranges into newly suitable regions, such as plants with long generation times. A climate-driven decline of late-successional plant species could lead to increased dominance of early successional species, or could leave ill-adapted plant communities that are susceptible to invasion by species that can thrive in the area's new climate" (Dukes and Mooney 1999:137). More troubling is that, as many invasive species become established, they have shown the ability to alter basic ecosystem properties in ways that feed back to affect many components of global change (Figure 5.15), creating

Table 5.4. Possible effects of global change factors on the prevalence of invasive alien species.

Elements of Global Change	Prevalence of Invaders
Increased atmospheric CO_2 concentration	±
Climate change	+
Increased nitrogen deposition	+
Altered disturbance regimes	+
Increased habitat fragmentation	+

Source: Reprinted from Dukes and Mooney (1999). Copyright 1999, with permission from Elsevier.

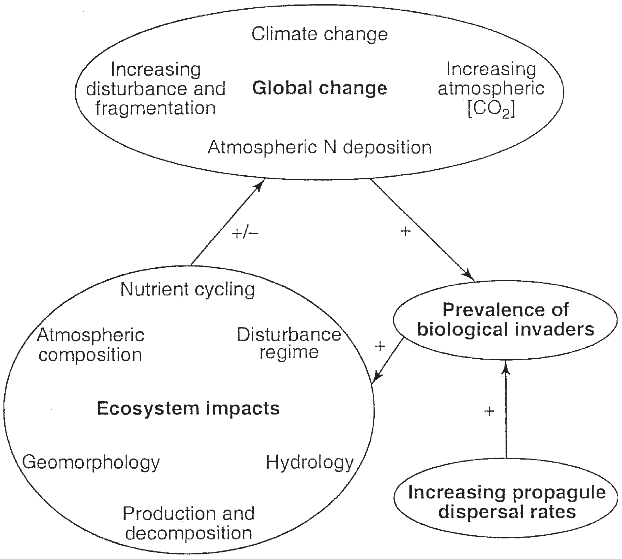

Figure 5.15. The impacts of global change on invasions, and feedbacks from invaders to global change. In this conceptual model, various elements of global change favor alien species, and changes in global commerce increase the rate of arrival of alien propagules. As alien species become more prevalent, they can alter ecosystem processes and properties, and such induced changes can interact with ongoing elements of global change. Feedbacks on global change can be positive (+) or negative (–), depending on the invading species and the ecosystem component or process affected. (Reprinted from Dukes and Mooney 1999. Copyright 1999, with permission from Elsevier.)

positive feedback loops that facilitate their permanent establishment.

Climate change can affect interactions among species. The Argentine ant (*Linepithema humile*), native to South America, is an aggressive invader in Mediterranean climates worldwide. In northern California, most native ant species cease foraging during the hottest days of summer, but the Argentine ant does not. If warming temperatures permit the Argentine ant to move into this region, it would have an immediate competitive advantage over native species through these increased foraging opportunities and could more rapidly displace them (Dukes and Mooney 1999:137).

5.4.3. Climate Influences on Ecosystem Structure

5.4.3.1. The Future of Coral in Warmer Oceans

Climate change in oceans causes: (1) changes in calcium carbonate saturation state (pH), (2) changes in sea level, and (3) changes in temperature of ocean water. As Ova Hoegh-Guldberg, a leading expert on marine biodiversity puts it, "… not all of these changes (in isolation) are likely to have a negative impact on marine biodiversity. The combination of these changes, however, is expected to drive major changes in the distribution and abundance of marine organisms" (Hoegh-Guldberg 2005:258).

As the level of CO_2 in the Earth's atmosphere rises, its rate of diffusion into the oceans increases. The buffering reaction of water, which can act as both an acid and a base in solution and thus effectively buffer an aquatic system from changes in pH, is affected by changes in CO_2 concentration as the following reaction occurs:

$$\begin{aligned}&\mathrm{CaCO_3 + H_2O \leftrightarrow CaCO_3 + CO_2}\\&\qquad \mathrm{+ H_2O \leftrightarrow Ca(HCO_3)_2 \leftrightarrow Ca^{2+} + 2HCO^-_3}\end{aligned}$$

As more CO_2 combines with water to form calcium carbonate ($CaCO_3$), there is reduced availability of bicarbonate ions (HCO^-_3) that can combine with H^+ ions, causing the concentration of H^+ ions to rise. pH, a measure of the negative log of the concentration of H^+ ions, therefore declines and the sea water becomes, by definition, more acidic. Thus the total carbonate alkalinity of seawater will decrease as carbon dioxide increases within the Earth's atmosphere. At the same time as this change is occurring, ocean temperatures warm and sea levels then rise as a result of the thermal expansion of this warmer water. Most global circulation models (GCMs) have predicted that oceans would warm slowly, even under maximum inputs of CO_2. In fact, ocean temperatures have increased more rapidly than expected, and surface waters have warmed faster than deeper waters. The heat content of the global ocean increased 2.3×10^{23} J between the mid-1950s and mid-1990s, representing a volume mean warming of 0.06°C, with surface waters (to 300 m) increasing 0.31°C in the same period. From 1997 to 1998, during the El Nino Southern Oscillation, ocean waters warmed to such an extent that 16% of the world's corals died.

The damage and death of coral reefs is significant to world marine biodiversity. The biodiversity of coral reefs worldwide is estimated at one million species of plants, animals and protists, all of these living within a total of only 400,000 km^2 of coral reefs (Hoegh-Guldberg 2005:262). But coral reefs have undergone major changes in the past 20 years as a result of climate change, and all to the detriment of their biodiversity.

The most common response in corals to increased ocean water temperature is called ***coral bleaching***. Although corals have been studied for over a hundred years, bleaching was never observed until the mid-1970s. Hoegh-Guldberg gives a precise description. "Coral bleaching occurs when corals rapidly lose the cells and/or the pigments of symbiotic dinoflagellates (zooxanthellae) that populate their tissues by the millions. Bleaching results in colonies turning from brown to white.... Reef-building corals that lose these important symbionts may experience mortality rates that exceed 90%. Mass coral bleaching events occurred in seven major episodes from 1979 to 2002, with concomitant losses of reef-building coral cover across thousands of square miles of coral reef" (Hoegh-Guldberg 2005:263–264). The Indian Ocean, for example, lost 46% of all corals in the El Nino event of 1997–1998 (Hoegh-Guldberg 2005:263–264).

The intensity and scale of current coral bleaching is unprecedented in recent history. Hoegh-Guldberg notes, in one study in Belize "… the mortality of *A. cervicornis* [a type of reef-building coral] in the 1990s left an unambiguous layer of coral branches in the sediments of reefs throughout the Caribbean. Aronson and his colleagues analyzed 38 cores from across the 375 km^2 lagoon basin, but no similar layer could be found in sediments stretching back at least as far as 3,000 years ago" (Hoegh-Guldberg 2005:265).

Warming of ocean temperatures might suggest that the distribution of corals will simply shift northward, as has been the case with many terrestrial species. But corals are ultimately light-limited because of their symbiotic relationship with photosynthetic algae. Thus, "however wonderful this scenario may sound (coral reefs off New York or Sydney), corals are ultimately limited by light levels and possibly carbonate alkalinity (which decreases in a poleward direction). These factors are likely to limit coral reefs to small changes in their latitudinal range" (Hoegh-Guldberg 2005:268). Analyses of current coral bleaching reveal that "thermal events that exceed 8 degree-heating weeks have almost always (99% of the time) resulted in coral bleaching. If conditions improve, bleached corals will recover their symbionts and hence their brown color.

If heating continues, however, and the degree-heating-weeks attains values of 13 or more, the event is likely to result in large-scale coral mortality" (Hoegh-Guldberg 2005:269).

Predictions of how much existing world corals will be affected by bleaching depend, in part, on the climate scenario employed by the model. But, even under a relatively mild scenario such as a doubling of carbon dioxide equivalents by 2100, bleaching would increase dramatically until it becomes an annual event by 2030–2050 for most parts of the world (Figure 5.16). As Hoegh-Guldberg puts it "… if the degree-heating-weeks of these future events is calculated, the values rise to well over 40 for most tropical oceans by 2100. … Given that major and almost complete mass mortality events occur for degree-heating-weeks values that exceed 13, it may be estimated that conditions such as those seen in the worst areas of the world's oceans in 1998 will be annual events by 2030–2050. Coral dominated ecosystems may become remnants of the past if sea temperatures continue to climb" (Hoegh-Guldberg 2005:269–270).

5.4.3.2. Loss of Polar Sea Ice: Implications for Polar Biodiversity

Based on predictions of all global climate models, the Intergovernmental Panel on Climate Change states that temperature increases associated with global climate change will be disproportionately higher in polar areas, particularly in northern latitudes (IPCC 2001; Räisänen 2001). The IPCC posits that, by the end of the twenty-first century, northern high latitude regions will experience temperature increases at least 40% greater than the global mean, and the central Arctic area will experience temperature increases 100% higher than increases in the global mean, an average increase of 3–4°C (IPCC 2001).

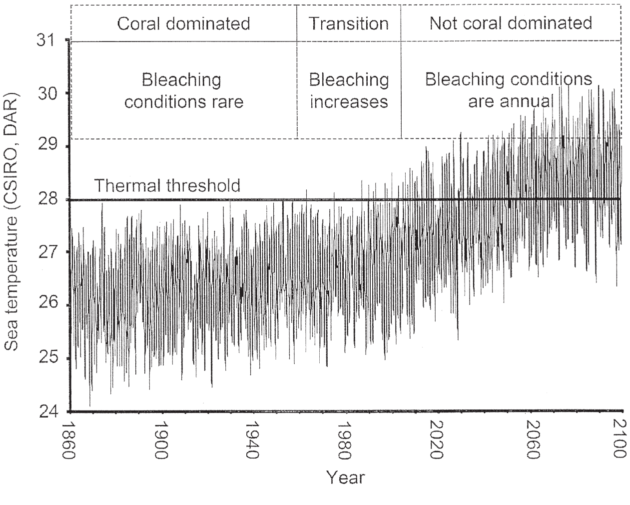

FIGURE 5.16. Projected sea temperatures in the central Pacific (Rarontonga, Cook Islands) from 1860 to 2100 using the CSIRO DAR model. The thermal threshold (horizontal black line) indicates the temperature at which corals and their symbiotic dinoflagellates begin to show bleaching effects at Rarotonga after 3–4 weeks exposure. Projected sea temperatures above the thermal threshold are used to predict changes in the frequency of bleaching and subsequent mortality of reef-building corals. (O. Hoegh-Guldberg. Yale University Press. Copyright 2005 by Yale University.)

These predictions are now being observed. Measurements of Arctic sea ice extent and thickness date to the late nineteenth century, although they have consistently improved in quality and coverage over time (Johannessen et al. 2004). Using the ECHAM4 GCM of the Max Planck Institute for Meteorology and the Hadley Centre's HadCM3 GCM of the United Kingdom Meteorological Office, which are then coupled to Arctic surface air temperature (SAT) data to produce coupled atmosphere–ice–ocean climatic models, Ola Johannessen of Norway's Nansen Environmental and Remote Sensing Center (NERSC) and his colleagues modeled potential Arctic temperature and resulting sea ice changes under a variety of scenarios and assumptions. After investigating multiple runs under various assumptions to determine if the present warming could be a natural anomaly, Johannessen et al. concluded that "no comprehensive numerical-model integrations have produced the present global warming anomaly … without including observed anthropogenic warming" (Johannessen et al. 2004:330). With Arctic warming has come declines in sea ice area (Figure 5.17a) and thickness (Figure 5.17b). The linear trend from 1978 to 2003 (Figure 5.17a) show an average reduction of 340,000 km^2 per decade, and a 7–9% per decade reduction in the area of multiyear ice (ice that survives at least one summer melt). September 2002 saw a record minimum end of summer ice cover unprecedented in 25 years of satellite records (Johannessen et al. 2004). Based on current data and trends, coupled with predictions from global climate change models, Johannessen et al. predict that summer Arctic ice cover may be reduced by 80% by the end of the twenty-first century "which could result in a nearly ice-free Arctic Ocean during summer at the end of this century" (Johannessen et al. 2004:337).

Reductions in extent and thickness of sea ice are significant to polar ecosystems because sea ice is a critical component of polar ecosystem structure. Many marine mammals such as seals, sea lions, and walruses (*Odobenus rosmarus*) need access to open water to feed. At the same time, they require ice in proximity to such open water of sufficient thickness to support adults and young, who are weaned in such ice areas close to open water. The primary predator of such mammals in the Arctic, the polar bear (*Ursus maritimus*) (Figure 5.18) also requires large areas offering this juxtaposition of ice and open water in order to find sufficient numbers of prey. In the Arctic's western Hudson Bay area, the ringed seal (*Phoca hispida*) has shown a pattern of declining recruitment from 1990 to 2001

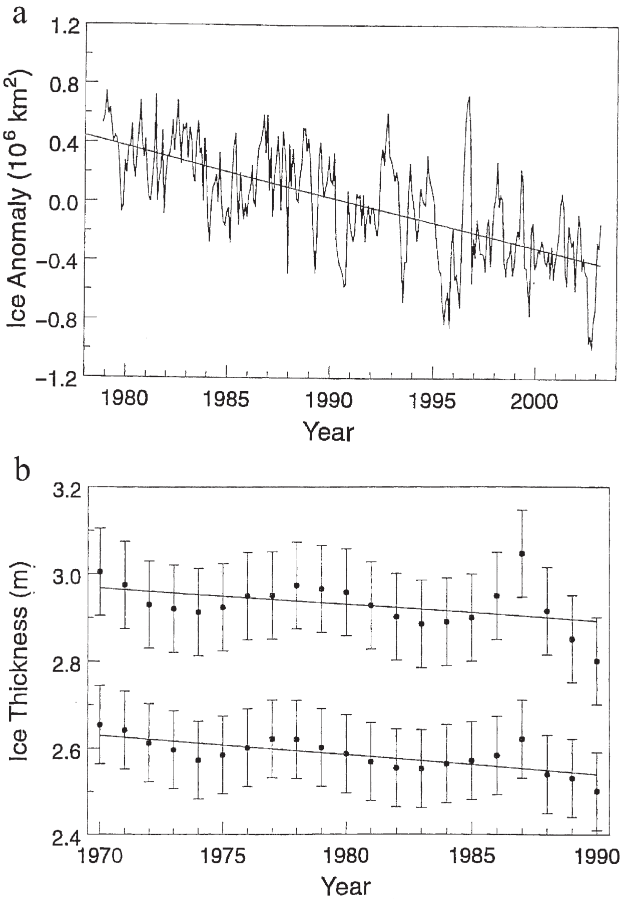

FIGURE 5.17. (a) Monthly departures (anomalies) of Arctic sea-ice area from historic means and seasonal cycles. From 1978 to 2003 the linear trend was -0.34×10^6 km^2 per decade. Note the largest anomaly of record-low ice cover in September 2002. (b) Interannual variability and linear trends for Arctic sea-ice thickness in winter (April, top) and summer (August, bottom). Error bars denote 95% confidence interval estimates for means of ice thickness. (O. M. Johannessen et al. 2004, Arctic climate change: observed and modeled temperature and sea ice variability. *Tellus*, © 2004 by Blackwell Publishing.)

FIGURE 5.18. The polar bear (*Ursus maritimus*) is an Arctic species showing increasing signs of stress and population reduction under current warming conditions. (Photo courtesy of Susanne Miller/US Fish and Wildlife Service.)

coincident with a climate pattern of declining snowfall, lower snow depth, warmer April–May temperatures and earlier breakup of spring sea ice (Ferguson et al. 2005).

If this pattern of decreased recruitment continues, the ringed seal, a principle prey of the polar bear, could see significantly smaller populations in the coming decades. The polar bear is remarkable among all mammals for its ability to fast for extended periods, not only during its winter denning period (during which all bears fast), but during non-denning periods when it is active. In Hudson Bay, for example, polar bears can prey effectively on marine mammals like the ringed seal only while ice is present adjacent to open water. Ice break up in Hudson Bay has historically occurred in late June, with the entire ice melt completed by late July, and polar bears then fast for four months until the fall ice freeze up in early November. In recent years (1962–2000), spring ice break up has advanced from 23 June to 30 May, with all ice gone by mid- to late June, adding 4–6 weeks of fasting to the polar bear's already challenging energetic regime.

The loss of sea ice has serious consequences for all polar bears, but it is particularly detrimental to females with cubs. Although female polar bears regularly make winter dens on land where they give birth to cubs, they also commonly make such dens on ice adjoining land (so-called "land-fast ice") as well as on drifting sea (pack) ice. Historically, pregnant females often choose to den on ice where the risk of human disturbance of the den is less, but unstable ice will often lead on-ice denning attempts to fail. Additionally, the ice must be covered with sufficient snow depth so that the female polar bear can construct an adequate den to nurse and protect her cubs.

Anthony Fischbach and his colleagues at the US Geological Service Alaska Science Center have monitored 89 radio-collared female polar bears and documented 129 denning events in northern Alaska and the Beaufort Sea from 1985 to 2005 using satellite telemetry (Fischbach et al. 2007). From 1985 to 1994, the proportion of dens on pack ice averaged 62%. From 1998 to 2004 it declined to 37%. Based on this decline, and on long-term observations of this large sample of polar bears, Fischbach et al. concluded, "The changing nature of the sea ice in the northern Alaska region appeared to be the major factor influencing the changing distribution of polar bear maternal denning that we observed. The significant landward shift from the early [1985 to 1994] to latter [1998 to 2004] periods appeared to be driven by reduced suitability of the pack ice as a denning substrate.… We conclude that the recent sea ice changes have collectively reduced the availability of offshore denning habitat" (Fischbach et al. 2007:1402).

These findings have implications for polar bear energetics. The Beaufort Sea population of polar bears has historically been able to spend their entire summers on sea ice, which, unlike the ice in Hudson Bay, never completely melted. Under these conditions, bears could forage efficiently for long periods and store large amounts of fat in preparation for winter. But recent recessions and losses of sea ice in the Beaufort and other Arctic seas force polar bears out over much deeper waters with lower productivity, forcing them to swim much longer distances to adjacent ice flows. These events can contribute to a negative energy balance in polar bears, or leave them stranded on shore where there is less prey available. Under these conditions, Fischbach et al. concluded that "most Beaufort Sea bears probably are not fat enough in mid-summer to fast for months and then den successfully without first returning to sea ice to feed.… Hence, in contrast to the Hudson Bay population, bears occupying the polar basin may be less capable of maintaining long-term reproductive viability by denning on land after a prolonged summer and autumn fast. Whether they are forced onto land or far offshore by the recent changes in sea ice, polar bear foraging opportunities in the Alaska region appear reduced from earlier times." (Fischbach et al. 2007:1403). Thus, it is now not surprising that biologists and other observers are seeing reduced physical size in adult polar bears and reduced fat deposits in both adult polar bears and cubs (Fischbach et al. 2007).

5.5. Conservation Planning and Climate Change: Creating Climate-Integrated Conservation Strategies

5.5.1. The Bioclimate Envelope: Modeling Climate Effects on Individual Species

Half a century ago ecologist George Evelyn Hutchinson defined the fundamental ecological niche as consisting of those environmental conditions under which a species can survive and grow (Hutchinson 1957). This so-called fundamental, or "Hutchinsonian niche" has been contrasted, in every textbook on general ecology and elsewhere, with the so-called "realized niche," that part of the fundamental niche the species *actually occupies* when constrained by the presence of and interactions with other species.

Part of the tolerable environmental conditions that comprise the fundamental niche, as shown earlier in the work of Joseph Grinnell, are climatic in nature. Thus every species has a "climate component" of its fundamental niche, or what could be referred to more directly as its ***climate niche***. Historically, biologists have seen, and some have carefully studied, the tendency of every species to track its climate niche through space and time in the face of changing climate conditions. For example, bird migration is one form of climate niche-tracking that is employed to cope with seasonal climatic variation.

Initially, interest in a species' climate niche, and the effect of climate change on a species, was investigated through small scale experiments that permitted investigators to make direct measurements to determine a species thermal tolerance, or how its biological rhythms and events might be changed in altered climatic conditions. For example, Francisca Saavedra of the University of Maryland (USA) demonstrated how the frequency and date of flowering could be advanced in an alpine wild flower, the two-lobe larkspur (*Delphinium nuttallianum*) by removing the snow from the soil surface where it germinated (Figure 5.19) (Saavedra 2002:218).

Saavedra's results are intuitive, but these and many other such studies form the foundation for the first steps in studying and modeling the effects of climate change on the Earth's biodiversity: the use of field experiments to determine correlations, physiological tolerances, and effects on biological timing associated with climate change that could then be used to estimate the climatic, especially thermal, tolerances of a given species. Studies like Sasvedra's form the bricks and mortar for building an understanding of a species' climate niche. The second step is then to develop atmospheric models that can predict future temperature changes within the species' range. If one can precisely define the climate niche of a species *and* predict how the climate will change over time within its historic range, one should be able to predict, and even comprehensively model, what will happen to the distribution of a species as climate changes. That is, one can combine data from the field experiments on the species and the knowledge of its current range with a regional atmospheric climate model to determine if a species would have to migrate in order to remain within its climate tolerances (Sanford 2002:169).

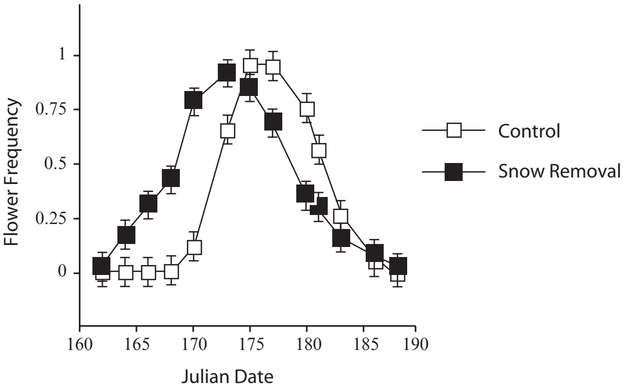

FIGURE 5.19. Flower frequency in relation to Julian date (Julian date 160 = June 9) in an alpine wildflower, the two-lobed larkspur (*Delphinium nuttallianum*) in response to snow removal at an elevation of 2920 m. Plots with snow removed flowered earlier in the growing season. Frequency values based on means of five plots per treatment. (From *Wildlife Responses to Climate Change: North American Studies* by S. H. Schnieder and T. L. Root, eds. Copyright 2002 by Island Press. Reproduced by permission of Island Press, Washington, DC.)

Today, when scientists integrate these data and concepts into an effective model, they can estimate the configuration of what has come to be called the ***bioclimate envelope*** of a particular species (Pearson and Dawson 2003:362). Bioclimate envelope models generally work by discriminating between the climates of locations inside and outside the ranges of a given species based on particular climate variables, such as minimum and maximum temperature. This strategy of modeling is technically known as a "correlative approach," and is used in a number of bioclimate envelope models, such as the Spatial Evaluation of Climate Impacts on the Envelope of Species (SPECIES), developed by bioclimatologists Richard Pearson and his colleagues (Pearson et al. 2002). The SPECIES model develops species-specific bioclimate envelopes based on observed species distributions integrated with five additional environmental inputs (derived primarily from climatic data, but including a measure of soil-type) (Pearson and Dawson 2003). Conceptually, the model is created through a series of spatial overlay maps, each with one of the five different attribute data (Figure 5.20).

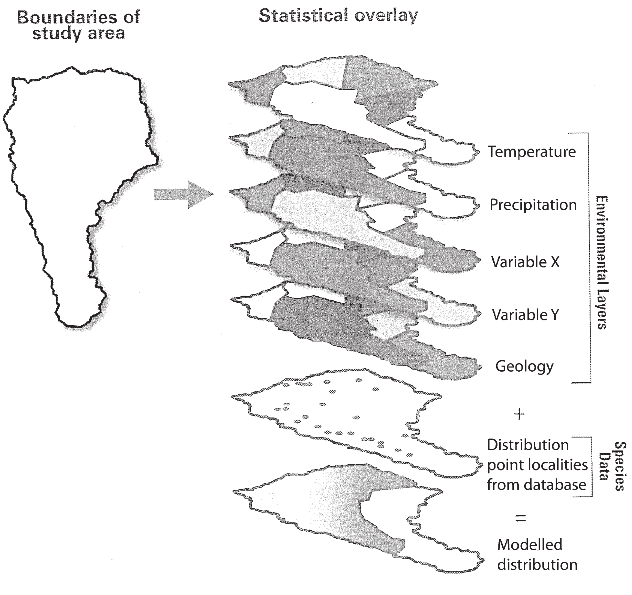

FIGURE 5.20. Schematic diagram showing the conceptual construction of a single-species range shift model. Maps of various attribute data (temperature, precipitation, geology, and other variables) are imposed over the study area. The actual species distribution (in this example, based on point locations from previously collected data) is then displayed within the study area and characteristics of attribute data are correlated with points where the species has been known to occur. The climatic attributes found at known locations are then applied to the entire study area, and the species total range is assumed to be wherever such climate attributes occur. Subsequently, if climate conditions change such that the correlated climate attributes shift to new locations, the species' range is assumed to shift with them. (A. T. Peterson et al., Yale University Press. Copyright 2005 by Yale University.)

Using models of bioclimate envelopes to predict future species ranges carries its own set of risks, not for the species but for the modelers. If the model's only information is that of climate projections and species climate tolerances, it will track the *potential future range* of the species, which will almost certainly be larger than its actual future range, just as a species' fundamental niche is almost always larger than its realized niche. To make the projection more accurate, the model must consider interactions with other species, the dispersal range and abilities of the modeled species, and the characteristics of the landscape through which it must disperse (i.e. landscape features and land use patterns) which may affect its dispersal rate and distance.

To understand and model which factors drive distribution, scaling factors become critical. At a continental scale, climate considerations will be dominant, such that only those areas where the species' climate tolerances match actual climate conditions can be considered potential occupiable range. However, that consideration alone will not produce accurate predictions of future species occurrence. The analysis must then move to regional and landscape scales that consider topography and vegetation (habitat). A subset of land area within the larger area of climate tolerance will represent areas where topography and land cover type are such that the species could occupy, while unsuitable topography and cover must be considered non-habitat. Finally, a still finer scale resolution should examine biotic interactions and microclimate conditions. For example, within the second subset of land cover with tolerable climate, is any of the area occupied by a competitor, predator, or parasite that would reduce, exclude, or eliminate the targeted species? If so, then these areas also, even though they possess tolerable climate and habitat, must be removed from the total estimate of suitable available habitat. Further, are there microclimate conditions, such as slope aspects (south or north), soil conditions (dry or hydric), or geologic factors (such as limestone, serpentine, or granitic rock bases) that could limit the occurrence of the species (Figure 5.21).

Visually, you can conceptualize how scale factors influence the model, and its predictions of species occurrence, in Figures 5.21 and 5.22. For example, one might be able to predict a species' occurrence under future climate conditions with climate data accurate to within 400 km^2 cells, but land cover estimates might need resolution to 5 km^2 cells, and biotic interactions, soil types, and geologic influences could require resolution to 1 km^2 cells or smaller (Figure 5.22) (Pearson and Dawson 2003). A species would need to find not only suitable climate conditions, but suitable land cover and sufficiently reduced competition from similar species to persist (Figure 5.22). For such analysis, fine scale resolution requires fine data resolution, making it harder to derive model predictions at smaller spatial scales. However, if such work is not done, coarse-scale model predictions may be inaccurate, and conservation

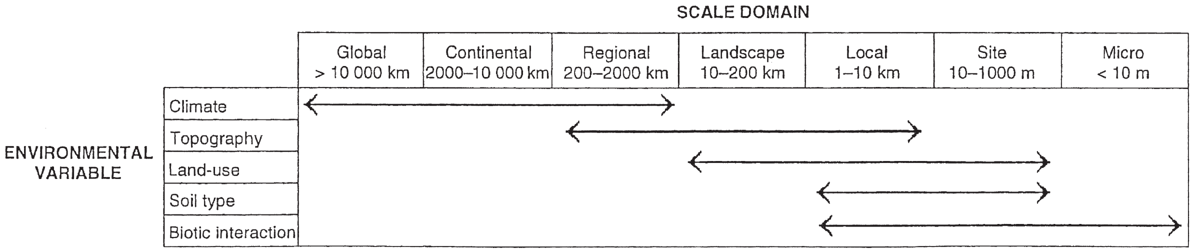

FIGURE 5.21. Schematic example of the scale domains associated with different biotic and abiotic environmental variables that could affect the distribution of species. The characteristic scale domains represent the scale at which a given factor is the dominant influence in species distribution. For example, climate is a controlling factor in distribution at global, continental, and regional scales, while biotic interactions become dominant controlling factors at local, site-specific, and microhabitat scales. (R. G. Pearson and T. P. Dawson 2003, Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, Copyright 2003 by Blackwell Publishing.)

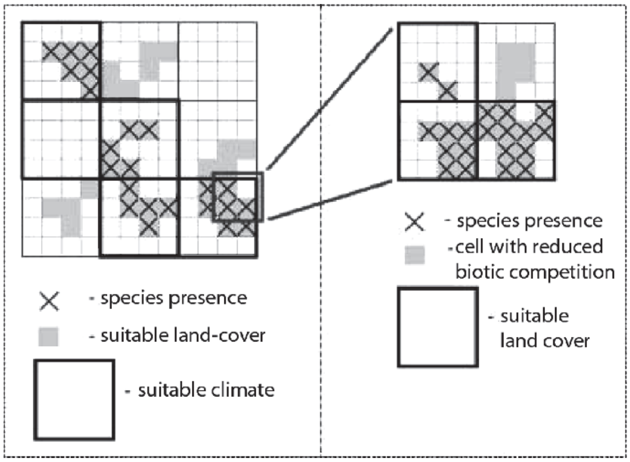

FIGURE 5.22. Conceptual example of nested scale domains within a hierarchical modeling framework. Different factors affecting a species distribution act at different scales. On the left, species occurrence (X) is limited to areas where both appropriate climate and landscape conditions are met. On the right, at a smaller spatial scale, species occurrence is further defined by sufficiently reduced levels of competition. (R. G. Pearson and T. P. Dawson 2003, Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, Copyright 2003 by Blackwell Publishing.)

plans based on inaccurate modeling will almost certainly fail. Now accurate measurements of dispersal abilities become critical because, as noted earlier, migration and dispersal are necessary to track the moving bioclimate envelope during a period of rapid climate change. Accurate modeling of landscape and topography also is essential because "the ability to migrate is a function not only of individual species' characteristics, but also the structure of the landscape over which dispersal is occurring, including the presence of natural barriers (such as mountain ranges) or the artificial fragmentation of habitats (through, for example, the growth of urban areas or deforestation)" (Pearson and Dawson 2003:365).

Despite these challenges, species envelop models are probably the best current tools for specific applications to conservation planning. Using knowledge of the climatic tolerances of individual species, such models try to predict where certain species, especially plants, could occur in the future under projected changes in temperature and moisture, or other climate variables, such as bioclimatologists Richard Pearson and Terence Dalton did for the stiff sedge (*Carex bigelowii*), among other species, in the United Kingdom and Ireland (Figure 5.23). These models of bioclimate envelopes, when combined with other types of modeling elements, can contribute to a constructive conservation response to climate change, the Climate Change-integrated Strategy.

5.5.2. Climate Change-Integrated Strategies for Conservation

Traditionally, conservation biologists have concerned themselves with theories of appropriate reserve size, shape and location as the questions of interest for successful biodiversity conservation, but have given little consideration to the effects of climate change in conservation strategy. In contrast, ***Climate Change-integrated Conservation Strategies*** (***CCCS***) represent a new but more and more widely adopted approach to the problem of climate change in which bioclimate envelope models are employed to develop effective conservation strategies to mitigate effects of climate change.

Conservation biologists who employ a CCCS integrate knowledge of species-specific bioclimate envelopes with five other tools: global climate models, regional climate models, dynamic and equilibrium vegetation models, land-use models, and site-specific sensitivity analysis. Models of global climate change provide broad resolutions of future climate change worldwide. Several are now accessible on the internet, such as those used by the Hadley Centre for Climate Prediction and Research of the United Kingdom's Meteorological Office

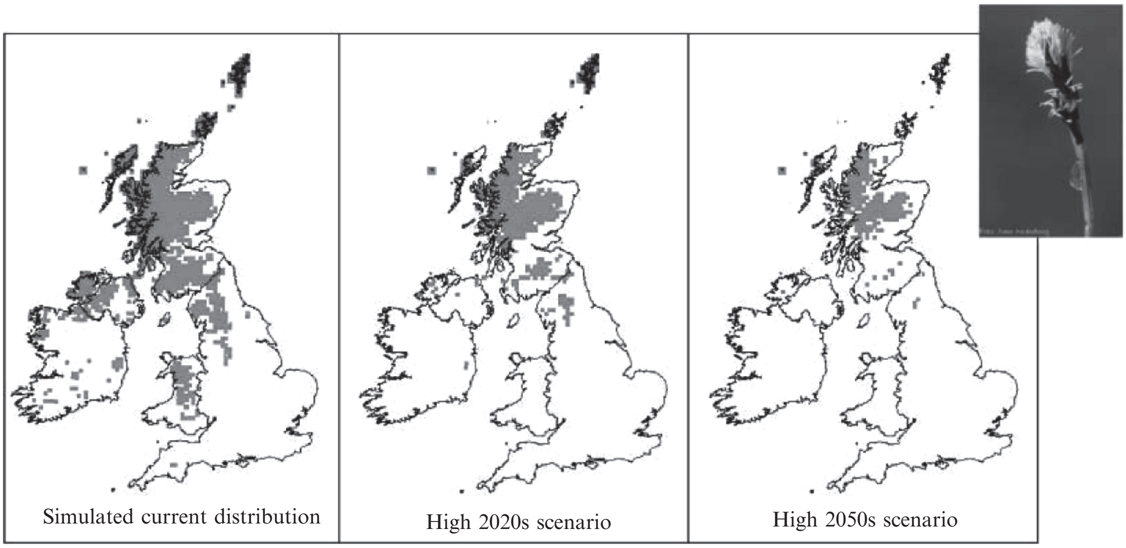

FIGURE 5.23. A simulated redistribution of suitable climate space for the stiff sedge (*Carex bigelowii*) in Great Britain and Ireland as predicted by the SPECIES model (Pearson et al. 2002), a bioclimate envelop model used to track a species climate niche through future periods of predicted climate change. Note, in this species, the concurrent projection for northward migration and overall range reduction. (R. G. Pearson and T. P. Dawson 2003, Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, Copyright 2003 by Blackwell Publishing.)

(http://www.meto.gov.uk/research/hadleycentre/models/modeldata.html), among others. With the right skills and software, a single scientist, working at a personal computer, can now compare simulated results from multiple models, thus gaining a sense of the degree of uncertainty associated with specific climate predictions. Regional climate models are embedded within GCMs to provide higher resolution results for particular areas, but their results are not as widely accessible, and they are not available for all regions. However, where such models exist and can be accessed, they form the bridge to the essential next step, the dynamic vegetation model.

Dynamic vegetation models provide insights into potential vegetation response to future climate change, either through the effect of climate change on successional processes (forest-gap models) or by assessing tolerances of plant communities or individual species to different climate conditions by combining the previously discussed bioclimate envelope models of all species in a particular region or biome. For example, see how the knowledge of the climate tolerances of one South African shrub, the Saldana pincushion (*Leucospermum tomentosum*), is integrated with projections of a global circulation model applied to the southern tip of South Africa (Figure 5.24). The projected range of this shrub is shown on the map in Figure 5.24 in black rectangles, and the difference between its current and predicted future range are apparent. Nevertheless, such projections must be evaluated further by coupling this projected distribution with a land use model that will show projections of what amount of the projected area

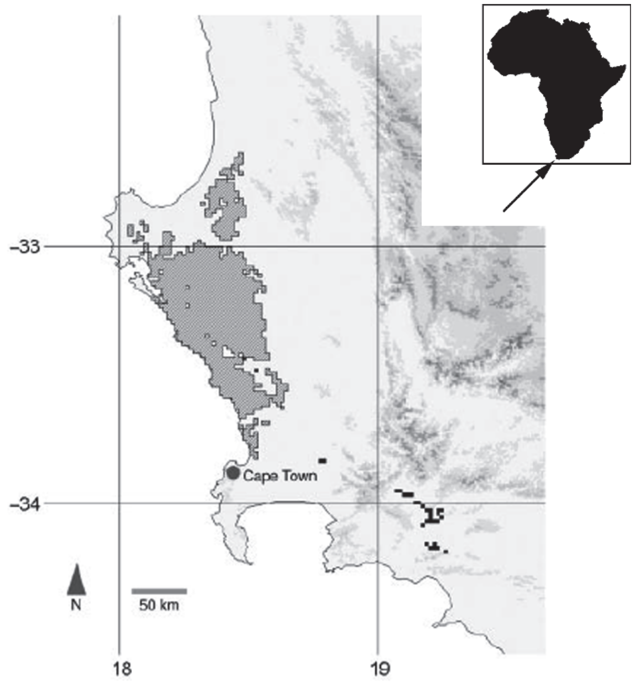

FIGURE 5.24. A bioclimatic model of predicted range shift of the South African shrub, the Saldana pincushion (*Leucospermum tomentosum*), is here integrated with projections of a global circulation model applied to the southern tip of South Africa. The projected range of this shrub (black rectangles), and the difference between its current range (shaded area) and predicted future range are apparent. (Hannah et al. 2002, Climate change-integrated conservation strategies. *Global Ecology and Biogeography*, Copyright 2002 by Blackwell Publishing.)

is actually *available* for use by the pincushion, and what has been transformed by human land uses that might make it unavailable for this species. As bioclimatologists Lee Hannah, Guy Midgley, and Diane Millar put it, "… a species whose potential climate envelope shifts into an area entirely dominated by agriculture or urban development may be faced with extinction" (Hannah et al. 2002:487). Ideally, the land use model also would incorporate land use features, such as rivers, mountain ranges, deserts, or other distinct physical features or biomes that might pose a barrier to the dispersal of the modeled species.

The final element of a CCCS is an integrative sensitivity analysis based on local ecology. Specifically, the purpose of the sensitivity analysis is to attempt to design management actions for conservation of target species in three ways: expansion of protected areas, management of the matrix of land and land use outside the protected areas, and regional coordination of management actions. In a perfect scenario, boundaries of protected areas would be expanded to encompass projected range shifts induced by climate change. Specifically, management in the protected area would follow a four-step process: (1) identification of conservation goals; (2) review of existing protected areas to assess what they contribute to such goals; (3) selection of additional areas needed to meet goals; and (4) implementing appropriate conservation actions in all protected areas.

Selection of new areas may require a comprehensive assessment identifying where target species are likely to occur that are currently unprotected (GAP analysis), and an assessment of potential new protected areas in terms of their relative conservation value, replaceability, and cost of acquisition, as was done for 343 species of Proteaceae, a plant family mainly restricted to South Africa (Figure 5.25).

Protected areas are not the only element of CCCS. Because species often must be able to shift ranges to adapt to climate change, the "matrix" of land around protected areas becomes critically important. Again to quote Hannah et al., "As changing conditions or extreme events alter conditions in protected areas, the matrix may contain the only available habitat (either spatially or temporally) for some species. Predicting when the matrix would come into play is fraught with uncertainties, so one of the best strategies is to maximize biodiversity-friendly land use in the matrix, including the option to revert human-orientated land uses to natural habitat. Conservation managers can prepare for future need for matrix habitat by preparing conservation agreements with landholders outside parks" (Hannah et al. 2002:492).

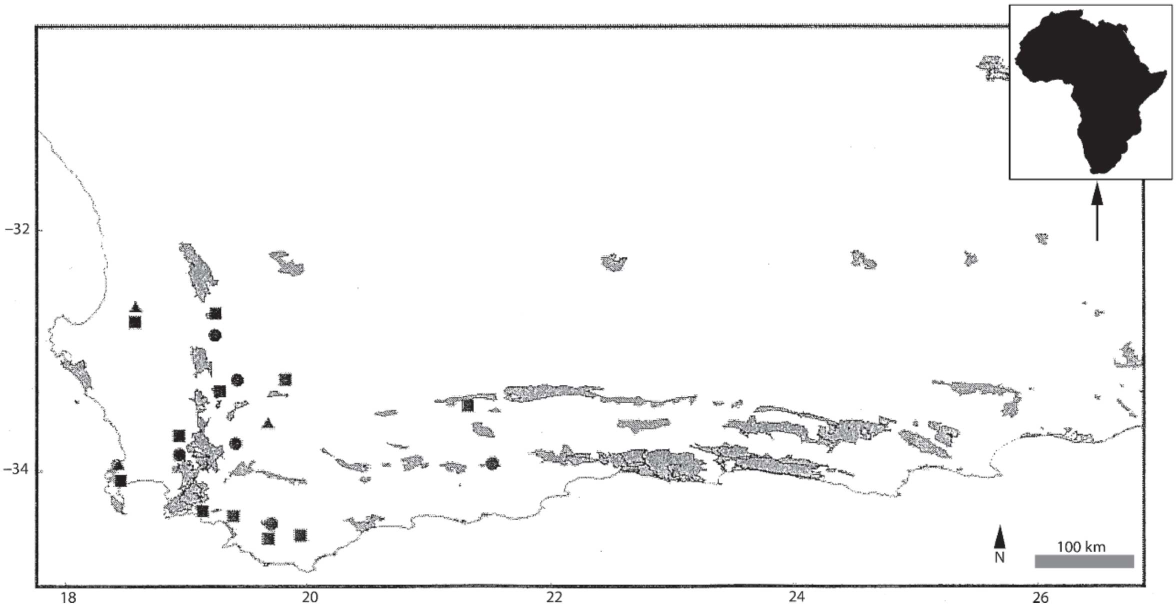

FIGURE 5.25. A GAP analysis showing present distributions (shaded areas) and projected future distributions for 343 species of the plant family Proteaceae in the Cape Floristic Province of South Africa, one of the world's greatest regions of endemic plant diversity, based on projections of Global Circulation Models applied to regional scales. Of the 343 species modeled, 217 had overlap between present and future projected ranges, with existing protected areas continuing to protect most of these species, but additional protected areas are needed to protect all species in the future, including areas that are irreplaceable for conservation protection (squares), areas that could be substituted for current protected areas at no additional cost (triangles), and areas that could be substituted for current areas at additional costs (circles). (Hannah et al. 2002, Climate change-integrated conservation strategies. *Global Ecology and Biogeography*, Copyright 2002 by Blackwell Publishing.)

What makes predictions about potential use of the matrix by individual species "fraught with uncertainties" is that biologists often know little about dispersal abilities of individual species. This is a critical point of ignorance because, as Pearson and Dawson recognized, "Sufficiently mobile species can be expected to track the geographical position of their bioclimate envelope through dispersal.… However, the ability of a species to migrate at a sufficient rate to keep up with the changing climate will be dependent on the dispersal characteristics of individual species, with future migration rates required to be at least equal to those of the early postglacial period.… Bioclimate envelope models do not account for species dispersal, but instead aim to predict the *potential* range of organisms under changed climate" (Pearson and Dawson 2003:365).

POINTS OF ENGAGEMENT – QUESTION 1

If modern refuges and preserves must mitigate the effects of climate change, what sorts of changes must be made in traditional approaches to reserve selection, reserve administration, and reserve mission for future reserves to be effective in this regard?

5.5.3. Modeling Efforts to Predict Future Responses to Ongoing Climate Change

The critical question for any modeling effort is, "how well does it work?" and, in this case, how do we know if it will work? The projected future conditions of the model have not yet occurred. Conservation biologists who spend their resources to preserve new areas identified by the model will have spent those resources in vain if they find, when the future has turned into the present, that their model was wrong. Therefore, current models must be evaluated for their degree of uncertainty and independently assessed in some way to evaluate the accuracy of their predictions. To understand this problem further, we examine some specific cases of modeling conservation planning for climate change, and the problems that can be latent within it.

Recent modeling efforts examining the relationship of climate change to species endangerment have not offered warrant for hope for the world's biodiversity. Jay Malcolm and his associates examined the possible effects of global climate change by integrating an array of GCMs with global vegetation models (GVMs) in an attempt to predict how vegetation communities worldwide would respond to projected climate changes. They found that, among locally endemic species, extinctions ranged from <1% to 43% (average 11.6%). The degree of biome specificity of a species had the greatest effect on extinction rate, with the most specialized species suffering highest losses. Among the world's designated "hotspots" where biodiversity is most concentrated (Chapter 4), the most vulnerable were the Cape Floristic Region (South Africa), the Caribbean, Indo-Burma, the Mediterranean Basin, Southwest Australia and Tropical Andes. In these areas, projected plant extinctions per hotspot sometimes exceeded 2,000 species (Malcolm et al. 2006). Working under the assumption that projected habitat changes would be attained within 100 years, species extinctions associated with climate change in hotspots in some cases exceeded extinctions caused by deforestation, thus making climate change an even more powerful threat to biodiversity than habitat destruction in some areas. In the model, endemic species with the most restricted ranges were the most susceptible to the effects of climate change. We can first refine and then apply the previously considered species–area relationship to see how species loss can be estimated in these cases.

Assume that the loss of a fraction Φ_A from the total area of habitat A_0 in a hotspot will lead to the extinction of the same fraction of the original species, S_0 that were present in the hotspot. Then, expressed as a function, species loss can be estimated as

$$f_{\text{lost–SAR}} = 1 - (1 - \Phi_A)^Z$$

where z is the species–area exponent and SAR is the species–area relationship.

Extinction in hotspots was generally no worse than in other areas, according to the models, but, as Malcolm et al. noted "Although it is encouraging … that these species rich regions did not appear to be unusually vulnerable to climate change compared with other areas, … it suggests that these high extinction rates can be extended to non-hotspot areas with similar collections of biome types (mostly tropical and subtropical in this case) and where species have similarly restricted ranges" (Malcolm et al. 2006).

One of the reasons for such wide estimates of potential extinction rates resulting from climate change is that Malcolm et al. incorporated no species-specific dispersal abilities into the models they constructed. Instead, they simply used two contrasting alternatives, "perfect migration," in which every species was assumed to be able to track its bioclimate envelope regardless of the distance or rate of movement required, and "zero migration," a scenario which assumed that species had no ability at all to move to new locations to adapt to climate change. Neither scenario is realistic for most species, and, when both are used in alternative model outputs, estimated extinction rates will show enormous variation. Another problem with such models is that they assume that present species distributions are in equilibrium with present climate, and that may not always be the case ((Peterson et al. 2005). Further, such models are not, so far, useful in predicting community behavior. As Townsend Peterson and his colleagues point

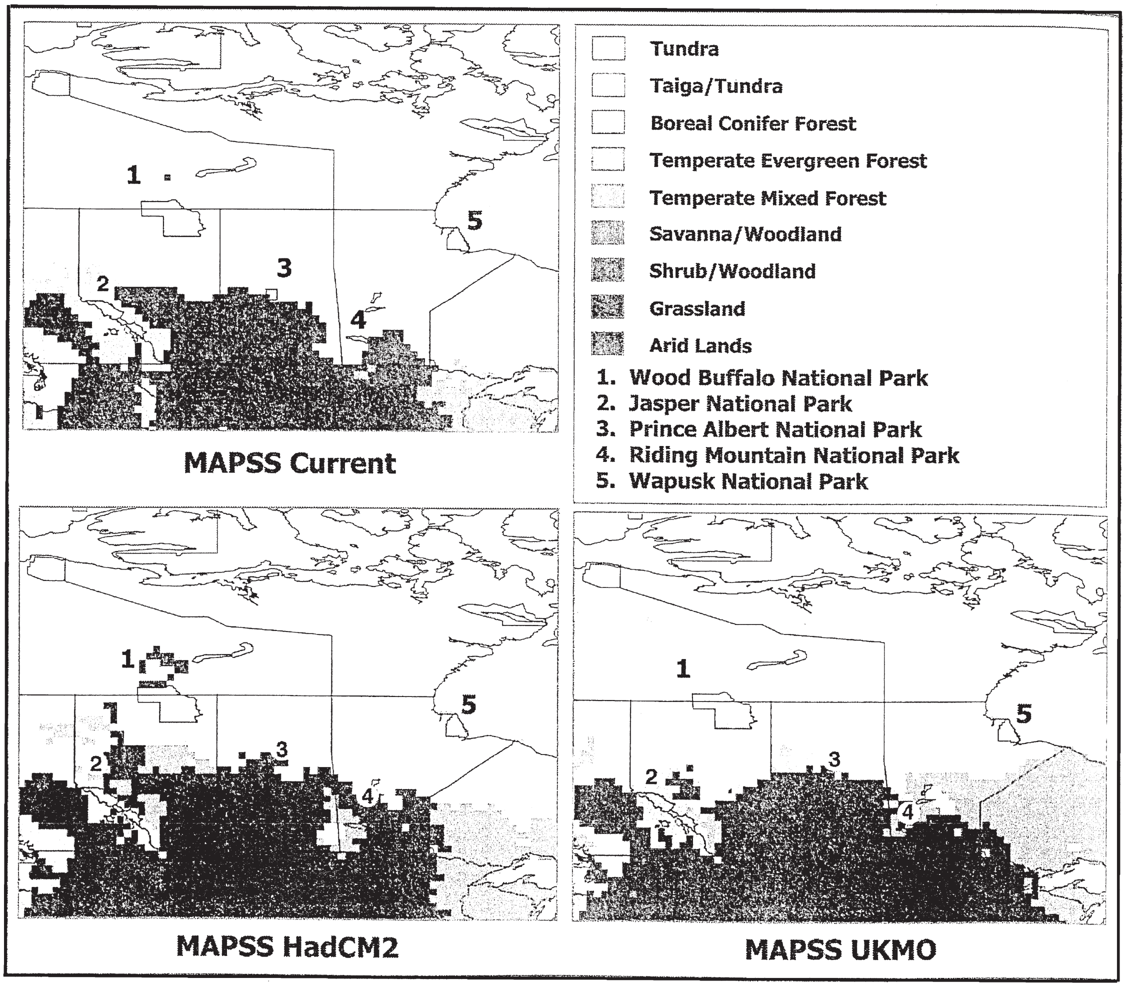

FIGURE 5.26. Modeled biome distribution of vegetation changes in the national parks of central Canada under two climate change scenarios of two different models, MAPSS HadCM2 and MAPSS UKMO. Note that in both scenarios, national parks experience overall declines in tundra and taiga biomes and increases in shrubland, grassland, and arid land. (D. Scott. Yale University Press. Copyright 2005 by Yale University.)

out, "… the idea of predicting the behavior of entire species assemblages under climate change scenarios based on community characteristics … appears untenable: species frequently show idiosyncratic responses to climate change …" (Peterson et al. 2005:217). Despite these obstacles, Canada has embarked on a comprehensive management plan to mitigate the effects of climate change in its national parks, anticipating that climate change will result in fundamental shifts in vegetation communities that the parts are designed to protect (Figure 5.26). Parks Canada has taken early initiatives to examine the implications of climate change for its parks and mandate. Since 2000, Parks Canada has commissioned a wide-ranging report on climate change impacts, developed climate change scenarios for each park, and conducted professional training workshops on climate change (Scott 2005:344).

Lack of data on species dispersive abilities, idiosyncratic behavior of species in ecosystems, and uncertainty in climate models all pose problems in making management plans for climate change. However, there are other concerns that are even more serious.

5.5.4. Errors of Application: Use and Misuse of Endangerment Criteria to Model Climate Change Effects on Biodiversity

Chris Thomas of the University of Leeds (UK) and 18 other scientists from Europe, Africa, South America, North America, and Australia conducted an extensive analysis of the projected changes in distribution of all endemic species in sample regions covering 20% of the Earth's terrestrial surface (Thomas et al. 2004), drawing on the familiar species–area relationship $S = cA^z$. Recall from Chapter 4 that S is the number of species in a given area, A is the area under consideration, c is a constant specific to a particular taxonomic group (for example, the relationship will be slightly different in reptiles than in mammals) and *z* is the "extinction coefficient" which integrates the rate of extinction in the group to the number of species in the area *A*. Theoretically, if we know the number of species in an area at time *t,* before climate change, and we can predict the amount of habitat loss resulting from climate change at time t_{+1} we should be able to predict the proportional species loss from *t* to t_{+1}.

To determine if the predicted habitat losses would lead to extinction or endangerment, Thomas et al. used the IUCN range criterion for extinction, namely that a species is considered "committed to extinction "if it has a projected future range of 0, critically endangered if its range declines by more than 80% in 50 years, endangered if it suffers range declines of 50–80% in 50 years, and vulnerable if it suffers more than a 50% decline in 100 years. Using these criteria with three climate projections (minimal, mid-range, and maximum-change scenarios), and two dispersal scenarios: universal dispersal and no dispersal, Thomas et al. estimated that 15–37% of species in sampled regions and taxa would be "committed to extinction" by 2050 (Thomas et al. 2004).

Models like those developed by Thomas et al. and others have been criticized for their inappropriate use of the IUCN's Red List of Endangered Species and the way in which IUCN criteria have been applied. H. Resit Akcakaya, senior scientist with Applied Biomathematics, and colleagues assessed the models designed by Thomas et al. and others in a comprehensive review published in 2006. "All recent studies" they wrote, "that we have reviewed that use the IUCN Red List Criteria to attempt to quantify likely extinctions from climate change have misapplied the Criteria … [and] these misapplications could … introduce substantial bias and uncertainty to projections of climate change impacts on biodiversity" (Akcakaya et al. 2006:2038).

To understand this critique more specifically, it is worth taking time to examine the problem in detail. Four of the five Red List Criteria are based on size and rate of population declines. The fifth (Criteria E) is based on quantitative models of extinction risk that could be produced from a population viability analysis or similar kind of tool (Table 5.5). Therefore, as Akcakaya et al. put it, "…only Criteria E includes quantitative thresholds for the risk of extinction. Because other criteria do not include such thresholds, the risk-based thresholds of Criterion E should not be used to infer an extinction risk for species assessed as threatened under any of the Criteria A-D. … The reasons for this are that, given the variation among species, it is not possible to validate the equivalence of the thresholds in different criteria, and the factors built into an evaluation under E, or under A-D may not be incorporated in the alternative criterion" (Akcakaya et al. 2006:2039–2039).

TABLE 5.5. An overview of the thresholds for IUCN Red List Criteria.

	Red List Categories			
Criterion	Critically Endangered (CR)	Endangered (EN)	Vulnerable (VU)	Qualifiers, Additional Subcriteria, and Notes
A1: past reduction in population size	≥90%	≥70%	≥50%	Over 10 years/ three generations, where causes are reversible, understood, and have ceased
A2: past reduction in population size	≥80%	≥50%	≥30%	Over 10 years/ three generations
A3: future reduction in population size	≥80%	≥50%	≥30%	Over 10 years/ three generations
A4: reduction in population size	≥80%	≥50%	≥30%	Over a 10-year/ three generation window, which includes the present
B1: small range (extent of occurrence)	<100 km^2	<5,000 km^2	<20,000 km^2	Plus two of (a) severe fragmentation/ few localities (1, ≤5, ≤10), (b) continuing decline, (c) extreme fluctuations
B2: small occupied range (area of occupancy)	<10 km^2	<500 km^2	<2,000 km^2	Plus two of (a) severe fragmentation/ few localities (1, ≤5, ≤10), (b) continuing decline, (c) extreme fluctuations
C: small and declining	<250 mature individuals	<2,500 mature individuals	<10,000 mature individuals	Continuing decline either (1) over specified rates and periods or (2) with (a) specified population structure or (b) extreme fluctuations
D1: very small population	<50 mature individuals	<250 mature individuals	<1,000 mature individuals	
D2: very small range	n/a	n/a	<20 km^2 or ≤5 locations	Capable of becoming CR or EX within a very short time
E: quantitative analysis (extinction risk)	≥50% in 10 years/ three generation	≥20% in 20 years/ five generations	≥10% in 100 years	Probability of extinction using quantitative models, e.g. population viability analysis

Source: Akcakaya et al. 2006, Use and misuse of the IUCN Red List Criteria in projecting climate change impacts on biodiversity. *Global Change Biology*, Copyright 2006 by Blackwell Publishing.

Akcakaya et al.'s point is that, if a species is judged endangered because of declining range size, a probabilistic "threshold of extinction" cannot be assigned to it using this criterion.

> *The most common mistake involves the time periods over which the decline rates and extinction risks are to be calculated. The IUCN Red List Criteria assess population declines over a period of 10 years or three generations (whichever is longer) up to a maximum of 100 years into the future. … Thomas et al. (2004) use the time scales of 50 years (for Critically Endangered (CR) and Endangered (EN) and 100 years for Vulnerable (VU)) to assess declines in future ranges of species, stating that the original time scales 'are not suited to evaluate the consequences of slow acting but persistent threats.' … It is misleading and incorrect to use these arbitrary time frames, especially when the generation times of the species being assessed vary. … In the Thomas et al. study, the animal species considered had relatively short generation times on average, so the overall effect of increasing the time scale is likely to have exaggerated estimates of extinction risk. … When time scales are changed and the thresholds are kept the same, the resulting set of rules loses this consistency, and cannot then be referred to as the IUCN Red List Criteria.*
>
> (Akcakaya et al. 2006:2039)

Akcakaya et al. also criticized studies for incorrect applications of spatial scales. "The IUCN Red List is explicitly a global assessment of projected extinction risk for species. Applying the IUCN Red List Criteria at sub-global scales requires special considerations.… When climate change impacts on species are assessed at a continental or smaller spatial scale, the projections for many species often exclude part of the species range. Models based on only a part of a species range cannot be used to assess global risk for that species, as they do not take into account the dynamics across the entirety of a species range" (Akcakaya et al. 2006:2039).

Akcakaya and his colleagues, although critical of such modeling efforts, write with a constructive purpose. They believe that a more practical use for the Criteria in this context is to identify species that are or might become threatened by climate change. Again, more specifically

> *… Criterion A3 is used to list species when there is a population reduction projected or suspected to occur in the future, based on an index of abundance appropriate to the taxon, or a decline in occupied habitat, range or habitat quality.… Although this is the most straightforward way to red-list species threatened by climate change, there are two issues to consider. First, this Criterion requires a projected reduction in abundance. Although this population reduction may be based on a projected decline in occupied habitat, range, or habitat quality, any assumed relationship between abundance and habitat/range must be justified.… Second, for short-lived species, Criterion A has limited time horizon (three generations or 10 years, whichever is longer). Because climate change can affect species in long time horizons (50+ years), three generations will often be too soon for the impacts of climate change to be apparent on these species, even if past greenhouse gas emissions have already determined (and have made inevitable) climate change effects in longer-time horizons. In most cases, however, uncertainty and lack of knowledge of environmental trends and demographic characteristics of species make it very unreliable to make predictions of extinction risk over periods longer than three generations.*
>
> (Akcakaya et al. 2006:2040–2041)

The quantitative thresholds used in the IUCN criteria are set against a common standard, based on expert review, to provide broad consistency between criteria and to allow comparisons across taxonomic groups. Therefore, Akcakaya and his colleagues recommend that "assessments of climate change impacts based on the IUCN criteria avoid arbitrary changes to the thresholds, and temporal and spatial scales specified in the criteria and associated guidelines." (Akcakaya et al. 2006:2041–2042)

POINTS OF ENGAGEMENT – QUESTION 2

As more and more species are threatened specifically by climate change, should the IUCN and other conservation organizations develop a category for "climate change – sensitive species"? If so, what criteria could be used to select species for this category, and what criteria should be used to determine if they are endangered by climate change?

5.6. Policy Initiatives for Climate Change and Conservation

Conservation responses to climate change need two components. The first, which we have explored at some length, is the strategy of adapting conservation strategies to deal with dynamic biodiversity and mitigate the overall effects of climate change. The second, less scientific and more political, is to engage policy makers to take action to reduce greenhouse gas emissions to levels that will keep biological changes manageable.

At this writing, the primary global instrument to attempt to regulate carbon emissions is the Kyoto Protocol, an agreement now affirmed by over 160 nations worldwide to attempt to limit carbon emissions. Although a commendable first step, the Protocol has glaring weaknesses and omissions that reduce its effectiveness in making progress toward its goal. Three of the world's most industrialized nations, Australia, Russia, and the United States, are not parties to Kyoto. Russia has indicated that it will sign in the future. Australia and the United States have indicated that they will not. The absence of these countries is significant, especially the absence of the US, the world's leading producer of greenhouse gases, including CO_2, of all individual nations.

Kyoto also is limited in its scope, in that, as conservation Reed Noss has noted, "Missing from the Kyoto discussions is any consideration of biodiversity" (Noss

2001:579). In forest conservation, for example, the protocol says nothing about forest conservation that is not directly related to carbon accounting. As noted earlier, vegetation, especially forests, can act as net carbon sinks by removing more atmospheric carbon for photosynthesis than they release in respiration. Carbon uptake, however, is greatest in relatively young, actively growing forest stands, such as could be created by forest plantations. But plantation forestry is not an effective path to biodiversity conservation. Again, Noss provides insight on Kyoto's relationship to conservation on this point. "Replacement of old trees with plantations is a "perverse incentive" of the Kyoto Protocol.… Simplistic carbon accounting, encouraged by the protocol, ignores the tremendous releases of carbon that occur when forests are disturbed by logging and related activities such as site preparation and vegetation management.… It ignores the fate of woody debris and soil organic carbon during forest conversion.… Typically, respiration from the decomposition of dead biomass in logged forests exceeds net primary production of the regrowth.… Considerable time is required – often hundreds of years – for regenerating forests to accumulate the carbon stocks characteristic of primary forests.… From the standpoint of maintaining biodiversity during climate change, conversion of natural forests to plantations cannot be justified" (Noss 2001:584–585).

Despite its flaws, the Kyoto Protocol does contain imaginative and potentially effective mechanisms for nation states, working together, to reduce carbon emissions. One example is the ***Clean Development Mechanism***, or ***CDM***, The CDM allows an investor in an industrialized country, whether industry or government, to invest in an eligible carbon mitigation project in a developing country and then be credited with ***Certified Emission Reduction Units*** (***CERUs***) that can be used by the investors to meet their obligations to reduce greenhouse gas emissions under the Kyoto Protocol (Watson 2005:385). In other words, even though Kyoto does not directly impose limits or reductions in carbon emissions on developing nations (an omission which is the basis for the charge that the protocol is unfair), it creates a mechanism in which industrialized nations or multinational corporations could stimulate carbon reductions in developing nations, primarily through technology transfer, and get the benefit of such reductions applied to its own account. Theoretically, if an industrialized nation used the CDM strategically, it could fulfill its obligations to carbon emissions reduction without actually reducing any emissions within its own borders. Although this use of the CDM might not be ideal for stopping global climate change, it speaks to another charge against Kyoto, that compliance to it will burden economic growth of industrialized nations by limiting their industrial efficiency and adding to their production costs. The CDM mechanism is such that, properly used, it could provide investors of industrialized nations with a way of making money from carbon reduction in developing nations.

In addition to this mechanism for trading emissions, the Kyoto Protocol also allows two other mechanisms of emissions trading. First, industrialized countries may trade their allocation of carbon emissions among themselves (Article 17). Second, industrialized governments or companies from industrialized countries may implement carbon mitigation projects jointly (Article 6) and then share the Emission Reductions Units generated to meet obligations to reduce greenhouse gas emissions, even if the reductions are not equally shared among the different countries (Watson 2005:385).

Most of the world's leading climatologists believe that Kyoto is only a first step toward stabilizing and ultimately reducing greenhouse gas emissions, and that it will take "many Kyotos" to ultimately develop a global strategy that will begin to make a difference. Nevertheless, individual nations, whether they are parties to Kyoto or not, can take steps to reduce carbon emissions. The three most effective strategies are increasing energy efficiency, using alternate, renewable sources of energy that have fewer or no carbon emissions, and developing techniques and technologies for carbon sequestration.

Increasing energy efficiency basically means achieving more work and production output per unit of energy input, such as increasing the mileage requirements for cars in a particular country or, at a household level, replacing traditional low efficiency incandescent light bulbs with high efficiency light bulbs. This chapter provides neither the scope nor the context to consider the myriad of ways that efficiency can be increased and energy saved, but all savings at all levels have the aggregate effect of reducing carbon emissions, and if conservation biologists can effectively persuade leaders of national governments to support policies that encourage or mandate such increased efficiency, they ultimately make such conservation a national habit and begin to reduce the stress of increased carbon emissions on global ecosystems.

Alternate sources of energy such as wind, water, geothermal, solar, and, in some cases, biofuels that generate less or no carbon emissions have much the same effect as energy efficiency, but with one significant advantage. Increased energy efficiency of conventional energy sources only reduces carbon emissions if the total overall use of energy remains static or declines. If total energy use increases, then increased efficiency simply reduces the *rate* of carbon emissions, not the *problem* of carbon emissions. For example, there is no net reduction in carbon emissions if new home building codes require insulation that conserves 50% more heat per unit volume, but builders, to satisfy the growing affluence of their clients, make the new houses twice as big. In contrast, alternative energy sources, especially those that produce no carbon emissions, have the potential for eliminating the emissions problem while still permitting an overall growth in energy use, and thus in productive capacity.

Carbon sequestration is perhaps the least familiar and still relatively untested form of reducing greenhouse gases, but the one that holds potentially the greatest promise. Already there are proven technologies for sequestration, such as injecting CO_2 produced in other kinds of industrial processes, into deep underground wells or beds of underground minerals so that it never enters the atmosphere. Biologist Thomas Lovejoy and climatologist Lee Hannah, who have studied the issue extensively, describe the process in some detail. “Injection involves pumping CO_2 at pressure into abandoned oil wells or saline (non-potable) aquifers. CO_2 injection is used commercially in oil recovery, and injection in saline aquifers has been proven. Mineral sequestration involves chemical reaction of CO_2 with rocks such as serpentine or peridotite that are abundant.… The processing required for this reaction is energy-consuming and refinements are needed to make it practical, but it offers the advantage of safe, compact storage …” (Lovejoy and Hannah 2005:393). CO_2 capture to feed these disposal options is not well tested, and would require a new generation of electric power plants with the ability to capture CO_2 even as it is produced. Some of these technologies have been tested, and, to a limited degree, actually work, but although such CO_2 removal has been proven possible it has not been demonstrated to be practical. The advantage of capture and sequestration is that is allows most of the current energy infrastructure to be maintained, greatly reducing costs, changes in energy production, and the time needed for transition. Therefore carbon sequestration could be a sound intermediate step, allowing rapid reduction of atmospheric CO_2. Sequestration offers the additional benefit of being able to drive down atmospheric CO_2 to pre-industrial levels (Lovejoy and Hannah 2005).

Overall, Lovejoy and Hannah advocate three steps toward a carbon neutral future that contain an immediate/short-term, medium-term, and long-term strategy. In the short term, implement improvements in energy efficiency and terrestrial biological sequestration (i.e. plant more trees!). As a medium term strategy, transition to increased reliance on renewable energy sources while increasing the sequestering of CO_2 produced from traditional fossil fuel sources. In the long-term, make a complete commitment and shift to supply all energy needs from renewable energy sources with no carbon emissions, such as solar power and wind power (Lovejoy and Hannah 2005:394).

5.7. Synthesis

The effects of climate change, long predicted, have, until recently, been thought to also be long delayed. Significant future events of climate change are undoubtedly ahead for planet Earth, but climate change is no longer a future scenario. It is an event whose time has come.

As if being a conservation biologist in the present world was not already discouraging enough, the prospect of climate change makes the whole effort seem, at first glance, perversely unfair. If the best laid local, regional, and global conservation plans can be swamped by unmanageable planetary forces of temperature, precipitation, sea ice retreat, and warming oceans, what is the use? There appears to be warrant for despair.

But if there is reason for despair in the face of climate change, there is also reason, indeed, necessity, for a far greater level of honesty about the human impact on the biosphere and the degree of fundamental change in human business and behavior that will be needed to change it. In the face of climate change, conservation can no longer be viewed as a kind of scientific recreational pastime. It never was that, but the reality of climate change effects completes the demolition of this myth. Conservation, to succeed, must address and encompass all aspects of human behavior and experience, including the way we heat our homes, the way we process energy, and the way we make a profit in a changing world.

Changes in the collective cultural behavior of the human species will come slowly, and it will do no good to put conservation plans on hold until the policy makers have fixed the climate problem. In the state and flux of imperfect, sometimes even misguided, policies, conservation practitioners must build the reality of climate change into all parts of their conservation strategies. The species whose historic habitat is being lost must be given opportunity, and, in some cases, direct help, to move to a place where it can still survive. The nature preserve and the national park may have to become dynamic, moving entities, defined by their connections instead of by their boundaries. And in the “non-preserve” world, humans will have to make room, and resources, for species to live where they did not live before.

Some species cannot move. Neither the top of the world nor the top of a mountain provide room for poleward migration or upward mobility, except into the mists of extinction, a place for the ghosts of biodiversity past who can no longer dwell on solid ground. For these species, their conservation *ex situ*, in the zoos and conservatories of the world, will take on new significance, as humans strive to perfect the skills to keep their race alive, until we have made the world good enough for them to live in again. But in a world of climate change, these are the elements that must form our climate of hope for the work of conservation biology.

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6

Genetic Diversity – Understanding Conservation at Genetic Levels

> *In the past two decades, a new field of conservation genetics has emerged with two general goals*: (*a*) *the precise description of genetic changes affecting population survival that occur during range and population contraction*; *and* (*b*) *application of genetic insight to successful management of threatened populations.*
>
> Stephen J. O'Brien 1996

In this chapter you will learn about:

1. **Why genetic concerns are central to the study of conservation biology**
2. **How to measure the genetic attributes of individuals and populations**
3. **Why inbreeding can pose threats to population persistence**
4. **The roles of hybridization and introgression in conserving biodiversity**

6.1. Genetics and Conservation: An Essential Integration

Conservation biology is a science concerned with the fate of populations, which are defined and identified by their genetic constituency. This unique genetic makeup not only distinguishes them from other populations, but also determines their capacity to adapt to changing conditions and, potentially, to produce new species. Many conservationists would argue that the conservation of genetic diversity is the foundational basis of all conservation efforts because genetic diversity is requisite for evolutionary adaptation, and such adaptation is the key to the long-term survival of any species (Schemske et al. 1994). To assure such survival, conservation biologists have two primary goals in the area of genetics. One is to preserve significant amounts of heritable genetic variation, particularly in small populations threatened with extinction. The other is to prevent the ***fixation of deleterious alleles***, a fixation that can contribute to reduced fitness and accumulation of harmful mutations (Lynch 1996). Preserving high levels of heritable variation helps to retain a population's current reproductive fitness and maintain its evolutionary potential, its capacity to adapt to environmental change over the long term. Preventing the fixation of deleterious alleles is intended to prevent declines in survivorship and fecundity that often occur in small populations as a result of reduced genetic diversity. Thus, the two goals are intimately related, and the overall aim and application of conservation genetics is to preserve species not simply as static forms, but as dynamic entities capable of responding to and coping with environmental change through time. Only when species possess this kind of adaptive potential do they have a reasonable expectation of persistence in a changing world, and only through maintaining their genetic diversity can they hope to possess this potential.

To achieve these goals, conservation genetics today encompasses three categories of activities: (1) genetic management of small populations to maximize the retention of genetic diversity and minimize inbreeding, (2) resolution of taxonomic uncertainties and delineation of management units based on genetic characteristics of populations, and (3) use of genetic analyses in forensics, especially in the enforcement of conservation laws and treaties, and in understanding the biology of target species. We will examine each category in detail in this and the next chapter to understand and appreciate the significance of the kinds of approaches and techniques that can be used in each of these categories. In this chapter, we will develop a conceptual understanding of conservation genetics, including its history, development, and theoretical framework. In the following chapter (Chapter 7), we will address more specific applications of genetic knowledge, skills, and techniques in actual conservation management. We begin with an overview of the foundations of conservation genetics.

6.2. Conservation Genetics and Conservation Biology

In the 1960s and early 1970s, even before conservation biology emerged as a distinct discipline, genetic concerns about small populations were growing. Moore (1962) and Hooper (1971) considered problems associated with inbreeding depression that could arise in populations confined to refuges. However, Hooper's conclusions minimized the risk of inbreeding by asserting that small amounts of immigration could stem inbreeding depression and that inbreeding itself facilitated the adaptation of local population subunits to particular environments. Small and declining populations also raised increasing concern over the potentially deleterious effects of ***genetic drift***, the random fluctuations in gene frequencies that occur as a result of non-representative combinations of gametes created during breeding. Geneticist R. J. Berry noted that loss of genetic variation through drift could limit future adaptation to environmental change, but ultimately concluded that natural selection would have sufficient strength to overcome the deleterious effects of genetic drift (Berry 1971).

Later investigators who examined the connections between genetics and conservation came to radically different conclusions. In Michael Soulé's classic review of potential genetic liabilities for small populations entitled "The Epistasis Cycle: A Theory of Marginal Populations" (Soulé 1973), Soulé noted six factors that account for loss of genetic variation in marginal populations: inbreeding, reduced gene flow with other populations, genetic drift, problems associated with ***effective population size*** (the size of an "ideal" population that would undergo the same amount of genetic drift as the actual population), reduced variation in niche width, and directional selection (Soulé 1973). Soulé demonstrated that, in populations of fruit flies (*Drosophila*), marginal populations rarely possessed novel or unique gene arrangements and many had reduced allelic diversity. Although Soulé made no explicit connections to conservation, he laid the foundation for what would become the principle genetic paradigm for concerns about small populations. "Marginal populations," wrote Soulé, "are … prone to severe reduction in numbers and can experience intermittent drift. Just a trickle of gene flow can, however, restore lost alleles; but, if the organism has poor dispersal powers, then marginal, isolated demes are expected to be allelically depauperate" (Soulé 1973).

The problems Soulé described are exacerbated in a demographic event known as a *bottleneck* (Frankel and Soulé 1981; Figure 6.1) in which a population declines to very low levels, which accompanying loss of genetic diversity. After a bottleneck, the remaining individuals, and their remaining genes, represent only a sample of the original source population. The smaller the sample, the more likely that it may not be representative of the source from which it was taken, and the more certain that some alleles, especially the rarer ones, may have been lost. This loss of genetic variation can mean a loss of heterozygosity in the population, which may be correlated with a loss of overall fitness (Frankel and Soulé 1981) because it exposes

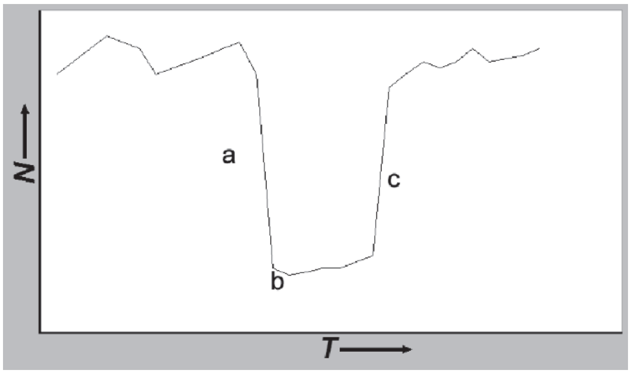


FIGURE 6.1. A graphical representation of population size before, during, and after a population bottleneck. *T* indicates time and *N* indicates relative population size. (Drawing by M. J. Bigelow.)

TABLE 6.1. Percent change in genetic variation and proportion of rare alleles lost from a population at bottlenecks (minimum sizes) of different magnitudes. Values of *p* represent proportions of each of four alleles.

Number of Individuals in Sample (*N*)	Percent Change in Genetic Variation	Proportion of Rare Alleles Lost	
		$p_1=0.70$, $p_2=p_3=p_4=0.10$	$p_1=0.94$, $p_2=p_3=p_4=0.02$
1	50.0	0.6300	0.7200
2	25.0	0.4950	0.6925
6	8.3	0.2125	0.5900
10	5.0	0.0925	0.5000
50	1.0	0.0025	0.1000
∞	0.0	0.0000	0.0000

Source: Developed from equations from Frankel and Soulé (1981). Table design by M. J. Bigelow.

a greater proportion of recessive genes in a homozygous condition, and traits previously masked are now expressed. Many of these recessive genes have deleterious or even lethal effects on organisms. Little genetic variation is lost if the reduction in population size is temporary, but significant genetic variability will be removed if the population remains small for many generations (Frankel and Soulé 1981; Table 6.1).

A second problem of small populations is that of genetic drift. Recall that genetic drift represents the random fluctuations in gene frequencies that occur as a result of non-representative combinations of gametes created during breeding. Geneticist Ian Robert Franklin provides one of the clearest definitions. “In a finite population,” wrote Franklin, “the array of genotypes is formed by sampling gametes from the previous generation; virtually all of the genetic effects which arise in small populations are an unrepresentative consequence of sampling, a process known as genetic drift” (Franklin 1980). Thus, genetic drift is to genetics what sampling error is to statistics. The smaller the population, the greater the probability that the sample (random matings of individuals) may represent neither the average nor the range of population characteristics.

A third concern regarding the genetics of small populations is ***inbreeding***, the mating of individuals having any degree of genetic relatedness. Inbreeding in a population often results in ***inbreeding depression***, a pattern of reduced reproduction and survival that occurs on account of inbreeding (Frankham et al. 2002:24). Based on theoretical arguments regarding inbreeding, Frankel and Soulé derived the ***basic rule of conservation genetics***, expressed as a percent change in the ***inbreeding coefficient*** (the probability that two alleles at the same locus in an individual are both identical by descent). The “rule” asserted by Frankel and Soulé (1981:73) is that natural selection for performance and fertility can balance inbreeding depression if the change in the inbreeding coefficient (ΔF) is no more than 1% per generation (Figure 6.2). The significance of this rule is well stated by the authors themselves: “We refer to the 1% rule as the ***basic rule of conservation genetics*** because it serves as the basis for calculating the irreducible minimum population size consistent with the short-term preservation of fitness” (Frankel and Soulé 1981:73, emphasis mine). Such short-term fitness preservation was considered safely achieved in most populations with an effective population size of 50 (Franklin 1980; Frankel and Soulé 1981). In contrast, long-term fitness was based on adaptation, measured most objectively in the ability of a population to speciate. Comparing long-term adaptive potential to short-term considerations regarding inbreeding, Franklin (1980) wrote, “In the long-term, genetic variability will be maintained only if population sizes are an order of magnitude higher,” (i.e., 500). Franklin based his “500 rule” on data compiled by geneticist Russell

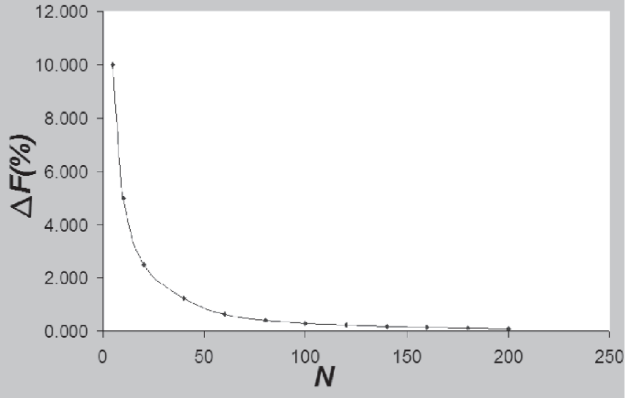


FIGURE 6.2. Percent change in the inbreeding coefficient (ΔF) at different population sizes (*N*). Note that the value of the inbreeding coefficient increases as population size declines.

Lande from mutation rates associated with *Drosophila*, maize, and mice. The figure of 500, noted Lande, may be roughly correct to "maintain typical amounts of heritable variation in selectively neutral quantitative characters," but should never be used as a "blanket application to species conservation" and should not be incorporated into species' survival plans when other factors have not been considered that might require larger populations for effective persistence (Lande 1988). Even as early as 1981, Frankel and Soulé, while citing Franklin's rule, noted that to accommodate continuing evolution, "the actual number of individuals that satisfy this criterion may be several times greater than 500" for a variety of reasons. They went on to argue against rule-of-thumb estimates and for continued genetic monitoring of endangered populations to determine if genetic variation was remaining at or above critical minimum levels (Frankel and Soulé 1981).

Despite its limitations, the "50/500 rule" was important to the development of conservation biology because it provided one of the first specific estimates of what constituted a "minimum viable population" or MVP. Although the term would not appear in published literature until a year after Franklin's estimates (Shaffer 1981), Franklin's efforts represented a first attempt to answer the question of minimum numbers needed for population persistence. Subsequent studies revealed increasingly complex relationships between genetics and demography, preventing any single rule of thumb from being used with certainty. In genetics, long-term inbreeding depression has been demonstrated in populations with effective sizes of 50–500, and may occur in larger populations as well (Latter et al. 1995; Frankham 1995a). Despite these limitations, conservation genetics provided the first paradigms, albeit initially little more than rough guidelines, for estimating minimum populations needed for species persistence.

Genetics was not established as a preeminent component of conservation biology only on the basis of theoretical argument. Soulé's earlier (1973) concern about some demes becoming "allelically depauperate" was dramatically supported with the publication of O'Brien et al.'s 1983 *Science* paper, "The Cheetah is Depauperate in Genetic Variation" (Figure 6.3). Most articles in scientific periodicals begin with objective, descriptive (and rather dull) titles, but the choice of such a vivid declarative sentence to entitle this investigation illustrated the authors' convictions about the veracity and significance of their findings. Specifically, an examination of 47 allozyme loci in 55 cheetahs (*Acinonyx jubatus*) from two isolated populations revealed no polymorphic loci and an average heterozygosity of 0.0 (O'Brien et al. 1983). The authors attributed this genetic uniformity in cheetahs to past population bottlenecks followed by severe inbreeding, and supported their explanation with data showing that sperm counts were ten times lower in cheetahs than in related felid species, and that 70% of the sperm were morphologically aberrant. Because the cheetah was an endangered species with a wild population estimated at less than 25,000 individuals, scientific interest was high and concern grew about loss of genetic diversity in wild populations.

FIGURE 6.3. Genetic samples of cheetahs (*Acinonyx jubatus*) have shown little genetic variation at sampled loci. Various studies have shown the cheetah to suffer higher-than-average rates of infant mortality, infertility, sperm abnormalities, and susceptibility to disease, all characteristics associated with high rates of inbreeding and low genetic variability. (Photo courtesy of Dawn Patrick and Cheetah Conservation Botswana.)

In skin tissue grafts among 14 cheetahs, 12 of which were between unrelated animals, all grafts were accepted beyond the rapid rejection stage, suggesting that the major histocompatibilility complexes (MHC) of individual cheetahs were identical (i.e., the grafts were the equivalent of receiving tissue from a genetically identical individual) (O'Brien et al. 1985). The authors asserted that lack of genetic variation contributed to increased susceptibility to disease in cheetahs (O'Brien et al. 1985). When an inbred population of lions (*Panthera leo*) in the Ngorongoro Crater in Tanzania underwent a population crash due to poor reproductive performance and high susceptibility to epizootics, it raised further concern that inbreeding depression was the cause of population decline (Packer et al. 1991).

Populations of concern to conservation biology, such as populations on islands, populations in fragmented habitats, and populations in zoos were examples that made conservation genetics important because genetic theory and measurement helped define critical applications as well as important theoretical puzzles to solve. We now turn to the science of such measurement, specifically targeted to solve the problem of how to measure the genetic diversity of a plant or animal population.

6.3. Measuring Genetic Diversity in Populations

6.3.1. Foundational Measures of Genetic Diversity

Precisely because genetic diversity is so important to population conservation, one must have reliable quantitative means of measuring it. Some measures of genetic diversity are identical to the measures of community diversity described in Chapter 4. For example, the Shannon Index (a measure of species diversity in a community) can be used with equal efficacy as a measure of genetic diversity if the proportional abundance of alleles is substituted for the proportional abundance of species. Likewise, the Simpson Index (Chapter 4), used as a measure of dominance in the assessment of community structure, can be used as a measure of expected heterozygosity (H_e) with the same substitution of allelic frequencies for species abundance (Vida 1994). Currently, there are three commonly used quantitative measures of genetic diversity. These are polymorphism, average heterozygosity, and allelic diversity.

Polymorphism refers to a genetic locus that has two or more forms (alleles). In a population or population subunit, polymorphism is expressed as the probability (P) of encountering a polymorphic loci among all loci in the population. To begin with a simple example, if a population has 100 genes and 50 of these have two or more alleles, the level of polymorphism is 0.50 (50%). More generally, we could say that P (polymorphism), for an individual or any larger group or unit, can be determined from the expression

$$P = \text{number of polymorphic loci/total number of loci.}$$

Although polymorphism is a concept that is easy to understand, it is not the most frequently used measure of population genetic diversity. That measure is ***average heterozygosity*** (H). Individual heterozygosity describes the observed proportion of heterozygous loci in an individual. Thus, individual heterozygosity is a measure of single-locus diversity. Average heterozygosity refers to the average proportion of individuals in a population that are heterozygous (carrying two different alleles) for a particular trait. This metric reflects the proportion of heterozygous individuals measured across several loci. We can calculate average hetereozygosity with the expression

$$H = \Sigma H_i / N$$

where H is the average heterozyosity at locus i and N is the total number of loci used in the estimate. Suppose there are four loci in a population. We will designate them (for lack of imagination) as 1, 2, 3, and 4. Now suppose that the frequency of heterozygotes for locus 1 is 0 (all individuals are homozygous for this locus), 0.3 for 2, 0.5 for 3, and 1.0 for 4. Then

$$H = (0 + 0.3 + 0.5 + 1) / 4 = 1.8 / 4 = 0.45.$$

Finally, the third measure, ***allelic diversity*** (A) refers to the average number of alleles per locus. It can be calculated at

$$A = \Sigma [A_1 + A_2 + \cdots + A_n] / N$$

where A_1 is the number of alleles at locus 1, A_2 the number of alleles at locus 2, and so on through all N loci.

Other measures can be used to describe populations, some derived from these foundations and others that are independent of them. Throughout the chapter, we will examine additional measures and their applications to describing genetic diversity. Keep these three introductory measures in mind as a foundation for new, more complex concepts and measurements that follow. Now we put the concept of heterozygosity (H) and allelic diversity (A) to immediate use in understanding two critical concepts affecting genetic diversity in small populations, bottlenecks and genetic drift.

6.3.2. The Loss of Genetic Diversity over Time: Bottlenecks and Genetic Drift

A ***population bottleneck*** is a "minimum population size as a result of a crash" (Frankel and Soulé 1981). The remaining individuals possess only a sample of the genetic variation present in the original source population. A bottleneck that lasts for only a short time has only minor effects on overall genetic variation, but one that persists for many generations will deplete genetic variability. Once depleted, genetic variation is slow to be restored even after the population recovers to a much larger size. Thus, current population sizes do not always correlate positively with the genetic diversity of a population if it has suffered one or more bottlenecks in the past. This loss of genetic variation can lead to a loss of heterozygosity, which, in some studies, has been correlated with a loss in overall fitness (Frankel and Soulé 1981). The correlation exists, as previously noted, because loss of heterozygosity allows a greater proportion of recessive alleles to occur in a homozygous condition so that traits previously masked are expressed. Many of these recessive genes have deleterious or even lethal effects on an organism.

Small populations that suffer a prolonged bottleneck may experience genetic drift. Genetic drift can occur in populations of any size, and is a normal evolutionary force that changes population gene frequencies through time. However, genetic drift usually has a greater effect in small populations because the proportion of such nonrepresentative matings tend to increase when the actual number of matings is low. The smaller the population, the greater the probability that the sample (random matings of individuals) may represent neither the average nor the range of characteristics found in the population. Genetic drift, which can be indexed by the change in frequency of a randomly selected allele, q, in one generation, can be estimated by the expression

$$\Delta q = \frac{q(1-q)}{2N_e}$$

where N_e is the variance effective population size, a concept we will examine in detail shortly. Thus, if the frequency of q is 0.2 and the effective population size is 100 the expected change in q (i.e. Δq) is 0.2 (1 – 0.2)/2 (100) = 0.16/200 = 0.0008, or eight one-hundredths of 1%. In contrast, if effective population size is ten, the effect on the same allele would be equal to 0.16/20 = 0.008 (eight-tenths of 1%). Both results represent very small effects, but notice the order of magnitude increase in the smaller population. If the population remains small and this relationship is reiterated for many generations, the effect of genetic drift on gene frequencies can become large.

Genetic drift can lead to a loss of heterozygosity or a fixation of deleterious alleles. These outcomes can cause random changes in the phenotype, and can lead to a decline in genetic variability (Franklin 1980). Such effects are exacerbated in small populations, particularly if they are closed to migration. In such a state, there is a decrease in the number of different alleles at a single locus in the population and in heterozygosity (Caughley 1994). The degree of decline in heterozygosity is a function of the population size, N, over the number of generations, t (Wright 1931). For example, over one generation, the amount of heterozygosity, H, changes this way:

$$H_1 = H_0\,[1 - 1/(2N)],$$

where H_0 represents the original level of heterozygosity (usually expressed as a proportion) and H_1 represents the new level of heterozygosity after one generation. Generalizing the equation for any number of t generations, heterozygosity declines as

$$H_t = H_0\,[1 - 1/(2N)]^t.$$

Note that the smaller the value of N, the greater the decline in heterozygosity. For example, a population of 50 individuals that began with a 0.5 level of heterozygosity would lose 1% of its heterozygosity in each generation (from 0.5 to 0.495). In contrast, a population of ten individuals with the same initial heterozygosity would lose 5% of its heterozygosity (from 0.5 to 0.475) (Table 6.2). Mutations can and do occur, and they increase genetic variability and heterozygosity, but this change in heterozygosity, ΔH, also is affected by population size:

TABLE 6.2. Heterozygosity and the effect of population size. The heterozygosity (H) of smaller populations declines at a faster rate than that of larger populations. Shown here are two populations: Population A with a starting size of 50 and Population B with a starting size of 10. Within one generation, Population B has declined to a level of 0.475. In contrast, it takes Population A 5 generations to decline to that level.

H_t	Population A (50)	Population B (10)
H_0	0.500	0.500
H_1	0.495	0.475
H_2	0.490	0.451
H_3	0.485	0.429
H_4	0.480	0.407
H_5	0.475	0.387

Source: Developed from data from Caughley (1994). Table design by M. J. Bigelow.

$$\Delta H = -H/(2N) + mH = H\left(m - \frac{1}{2N}\right),$$

where m is the addition of heterozygosity through mutation, typically expressed as a rate. Populations reach an equilibrium level of heterozygosity ($\Delta H = 0$) at

$$H^* = 2Nm.$$

The smaller the size of the population, the lower its equilibrium heterozygosity.

Genetic drift and population bottlenecks can combine to produce long-lasting effects on populations, even after numerical recovery. Consider the Mauritius kestrel (*Falco punctatus*) (Figure 6.4), a small, rare falcon found only on the island of Mauritius in the southwestern part of the Indian Ocean, east of Madagascar. Following declines associated with the use of pesticides and the destruction of its habitat from deforestation throughout the 1960s and early 1970s, this population is believed to have been reduced to a single breeding pair in 1974. Through careful protection, habitat restoration, and managed breeding that was part of an intensive conservation and recovery program from 1983 to 1993, the population had been restored to over 200 individuals by 1994 (Figure 6.5a), and to 400–500 individuals, and over 200 breeding pairs, by the late 1990s (Groombridge et al. 2000). By examining DNA from living kestrels and comparing it to the same DNA loci in museum skins of kestrels from ancestral populations, Jim Groombridge and his colleagues documented the loss of genetic diversity that has accompanied this population bottleneck. Overall allelic diversity has declined by 57%. A number of unique alleles present in the ancestral population are no longer extant in living kestrels (Figure 6.5b) and the restored population shows a 57% reduction in heterozygosity (Table 6.3) Despite these genetic scars, the population has continued to increase, and its productivity, indexed by the average number of fledglings per nest, rose 31% from 1994 to 1998, even after intensive management

FIGURE 6.4. The Mauritius kestrel (*Falco punctatus*), a species found only on the island of Mauritius in the Indian Ocean, displays classic evidence of loss of genetic diversity following a severe reduction in population size (population bottleneck) during the 1960s and 1970s. (Photo courtesy of The Mauritius Wildlife Foundation.)

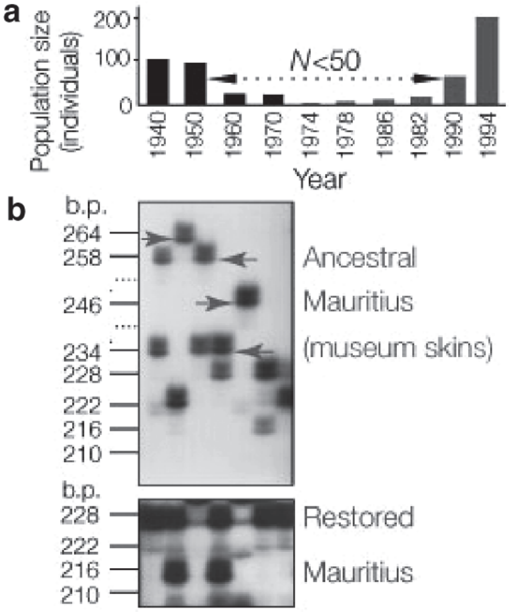


FIGURE 6.5. (a) The population size of the Mauritius kestrel (*Falco punctatus*) from 1940 through 1994. Note the severe reductions beginning in the 1960s when the population declined and remained at less than 50 individuals. (b) DNA fingerprints (microsatellite genotypes) from Mauritius kestrel museum skins (top) compared to DNA from the same region in birds from the restored population (bottom). "b.p." refers to specific DNA base pairs. Dark bands represent the presence of specific alleles. Note the reduction in the number of bands in the restored population, indicating reduction in allelic (genetic) diversity. (Reprinted by permission from Macmillan Publishers Ltd: *Nature*, Groombridge, J. J., C. G. Jones, M. W. Bruford, and R. A. Nichols 2000. 'Ghost' alleles of the Mauritius kestrel. *Nature* 403:616. Copyright 2000.)

TABLE 6.3. Genetic diversity of the Mauritius kestrel and other kestrel populations. Mean numbers of alleles (A) and average heterozygosity (H_e) of the restored (post-bottleneck) Mauritius kestrel population compared with those of the ancestral (pre-bottleneck) population and with other kestrel population. Note that with the exception of the Seychelles population, which also suffered severe population reduction, the ancestral Mauritius kestrel population had less genetic diversity than other African and European kestrel populations. With further reductions in the restored population, the differences are now even greater.

Species	A	H_e	Sample Size
Endangered			
Mauritius kestrel			
Restored	1.41	0.10	350
Ancestral	3.10	0.23	26
Seychelles kestrel	1.25	0.12	8
Non-endangered			
European kestrel	5.50	0.68	10
Canary Island kestrel	4.41	0.64	8
South African rock kestrel	5.00	0.63	10
Greater kestrel	4.50	0.59	10
Lesser kestrel	5.41	0.70	8

Source: Reprinted by permission from Macmillan Publishers Ltd: *Nature*, Groombridge, J. J., C. G. Jones, M. W. Bruford, and R. A. Nichols 2000. 'Ghost' alleles of the Mauritius kestrel. *Nature* 403:616. © 2000.

had ceased. Although such increase is a hopeful sign, one must remember that, in every population, there are some genes, known as ***lethal genes***, which, although recessive and unexpressed in a heterozygous state, will, in a homozygous condition, always result in the death of the individual. The proportion of such genes in a population, its ***lethal load***, often rises when alleles are lost during a period of population reduction. As alleles are lost, heterozygosity is reduced, as in the Mauritius kestrel, and the probability of homozygous expression of such lethal genes is higher if they are present. The sampling of genetic material present in the founders represents a random sample of the population's genetic variability, but, in small founder groups, the genetic constituency of the founders may or may not be representative of the population. In this case, if the last remaining pair of kestrels possessed lethal genes, their expression is likely to emerge in future generations and depress population survival rates. But, if such lethals were not present in these founding individuals, the population is not exposed to this risk.

The case of the Mauritius kestrel suggests that wild populations may be highly resilient to genetic loss, and provides hope that conservation efforts can be successful even after severe reductions in numbers and loss of genetic diversity. In fact, recent genetic studies of multiple species suggest that low levels of genetic variation are not necessarily an indication of population endangerment (Zhang et al. 2002). Nevertheless, the case of the Mauritius kestrel reveals that population reductions can have effects on genetic diversity which do not rapidly disappear with increases in population size alone.

6.3.3. Genetic Drift and Effective Population Size

The theoretical consequences of genetic drift are normally calculated for an "ideal" population in which each individual contributes gametes equally to a genetic pool from which the next generation is formed. Real populations rarely conform to this happy genetic vision. Instead, we must be able to estimate the *effective population size*, N_e, which represents the size of a randomly mating population that is subject to the same degree of genetic drift as a particular "real" population. Another way to say this is that the effective population size of a real population is equal to the size of an ideal population that has the same amount of variance in allelic frequencies. Hence, the effective population size, defined in this way, is more correctly called the "variance effective size." In contrast, the effective population size of a real population also can be defined, and estimated, as size of an ideal population that has the same level of inbreeding, which is then more precisely referred to as "inbreeding effective size" (Loew 2002:242). Regardless of which measure is used, the effective population size of any population is affected by a number of variables, including variance in progeny number (brood or litter size), differential sex ratios, fluctuations in total numbers, and deviations from random mating systems (Frankham 1980). The first three problems can be evaluated separately if we assume that mating is random.

To examine the effect on N_e of variation in the number of progeny, let N equal the population's actual size (census size) and σ^2 the variance in progeny number. Then

$$N_e = \frac{4N}{2+\sigma^2}.$$

Thus, if the size of the population is 100, brood size ranges from 0 to 8 and the variance is 4, the effective population size (N_e) is 400 divided by 6, or 67, which is one-third less than the census population size. Effectively, an equalization of family size in a population should lead to an approximate doubling of the effective population size. This prediction has proven true in experimental tests. In *Drosophila*, populations subjected to equalization of family size had greater genetic variation and greater reproductive fitness than populations in which family size was not equalized (Boriase et al. 1993).

For populations with unequal sex ratios, the effective population size is

$$N_e = \frac{4\mathrm{N}_m N_f}{\mathrm{N}_m + \mathrm{N}_f}$$

where N_m is the number of males and N_f is the number of females. Consider a population of 100 elk (*Cervus elaphus*) (Figure 6.6). If there are 50 reproductive bulls and 50 reproductive cows, each bull mates with one cow, and each pair represents a unique association of individuals, then the effective population size is 10,000 divided by 100, or 100. But there is no wild elk population anywhere with such a sex ratio, nor are there any that use such a mating system. Through natural selection and the effects of sexually differential hunting pressure, wild elk populations have more females than males. In autumn, during the breeding period or "rut," males gather groups of females ("harems") that they defend against other males for exclusive breeding privileges. Suppose, in such a setting, that the breeding population of 100 elk is actually composed of 10 males and 90 cows. Each male takes a harem of 9 females and successfully defends it from other males. This scenario is a gross simplification of what really happens, but it is a little closer to real elk life. In harem-mating systems, the relatedness of offspring born to females within a harem is higher than the relatedness of offspring from females of different harems. Thus, in this revised scenario, the effective population size is 4 × 10 × 90 divided by 10 + 90, or 3,600 divided by 100, producing a result of 36.

FIGURE 6.6. Elk (*Cervus elaphus*) are an example of a species with a harem mating system that reduces the effective population size. (Courtesy of U.S. National Park Service.)

Here the effective population size of a population with a biased sex ratio is about one-third that of a monogamous population with a balanced sex ratio. Thus, the sampling error (genetic drift) associated with random mating in a population of 36 individuals is equivalent to the sampling error associated with mating in a population of 100 individuals with the sex ratio and mating system just described, and would lead to increased rates of inbreeding. Studies by Briton et al. (1994) have confirmed this prediction. Polygamous mating systems associated with unequal sex ratios increase rates of inbreeding and loss of genetic variation, leading Frankham (1995a) to assert that harem breeding structures should be avoided whenever possible in captive breeding programs.

Effective population size also changes when populations fluctuate. If population size varies from generation to generation, then the effective number is the *harmonic mean* (the reciprocal of the arithmetic mean of the reciprocals of a finite set of numbers):

$$\frac{1}{N_e} = \frac{1}{t}\left(\frac{1}{N_1} + \frac{1}{N_2} + \cdots \frac{1}{N_t}\right),$$

where N_t is the effective size of the population at generation t. It can also be expressed as:

$$N_e = t / \sum (1 / N_{e_i}),$$

where N_{e_i} is the effective population size in generation i.

POINTS OF ENGAGEMENT – QUESTION 1

Work out the mathematics of the effective population size for 10 generations with a population of 100 in every generation, then repeat the calculation a second time, letting one generation "crash" to 10 individuals. What happens to the effective population size?

Like effects of unequal family sizes and unequal sex ratios, unequal population sizes should lead to increased levels of genetic drift and loss of heterozygosity. These predictions have been verified experimentally (Woodworth et al. 1994).

All of these formulas assume random mating, but that assumption is often violated in real populations. More complex mathematics are required to determine effective population sizes where there is significant deviation from random mating. Even if random mating is approximated, however, most populations will have a lower genetically effective population size than their census size. The problem of genetic drift becomes especially important when the effective population size is small. When the effective population size is large, the expected variation in a typical genetic character is determined mainly by the strength of selection for or against that character (i.e. genetic variation is determined by mathematical probability). When effective population size becomes less than a few hundred individuals, expected variation of the character becomes largely independent of the strength of selection and is determined primarily by the balance between mutation and drift (i.e. variation is determined by random events).

6.3.4. Bottlenecks, Small Populations and Rare Alleles

Although bottlenecks have little effect on genetic variability in a population unless the population remains small for a long time, the effect of size reductions on rare alleles is a different matter. Rare alleles can be lost quickly in small populations that experience a sudden decline or that remain at low levels for extended periods. The expected number of alleles, $E(n)$, remaining after a genetic bottleneck is equal to

$$m - \sum (1 - p_j)^{2N_e}$$

where m is the number of alleles prior to the bottleneck, p is the frequency of the jth allele, and N_e is the effective number of individuals at the bottleneck. Suppose that $m = 4$ and that one allele is common, but the other three are rare. Look what happens to the average number of alleles (Table 6.4) as the effective number of individuals drops from 50 to 1. The rarer an allele is, the more likely that it will be lost (Frankel and Soulé 1981).

The earliest paradigms of modern conservation biology arose from concerns about long-term loss of genetic variation in small populations, leading to one of the earliest stated goal of conservation biology: the retention of 90% of a population's genetic variability for 200 years (Soulé et al. 1986). The loss of genetic variation is reduced (and the probability of meeting this goal improves) as the effective population size grows to an effective population size of about 1,000 individuals. Beyond this level, further increases in effective population size do not usually increase the amount of genetic variability in the population (Lynch 1996). But effective population size is often only one-tenth to one-third the number of breeding adults in the population for reasons noted previously, including unequal family sizes, unequal sex ratios, and unequal population sizes over time. Thus the $N_e > 1{,}000$ criterion suggests the need for a stable population of 3,000–10,000 breeding adults in each generation to prevent long-term loss of genetic variation.

TABLE 6.4. Decreasing population size influences the average number of alleles. In this case, four alleles are observed – one with a high frequency and three with lower frequencies. Rare, less common alleles are more likely to be lost during a bottleneck. These rare alleles are typically not essential in the initial environment. However, as the environment changes they might be crucial for survival.

	Average Number of Alleles Retained, Given the Original Frequency of Allele	
Effective Number of Individuals (N_e)	$p_1 = 0.70$, $p_2 = p_3 = p_4 = 0.10$	$p_1 = 0.94$, $p_2 = p_3 = p_4 = 0.02$
∞	4.00	4.00
50	3.99	3.60
10	3.63	2.00
6	3.15	1.64
2	2.02	1.23
1	1.48	1.12

Source: Developed from equations by Frankel and Soulé (1981). Table design by M. J. Bigelow.

6.4. The Problem of Inbreeding

6.4.1. What Do We Mean by "Inbreeding" and How Would We Measure It?

As if the problem of finding a mate was not enough, individuals in small populations may suffer just as much or more as a result of finding the *wrong* mate. More specifically, they are likely to mate with close relatives with whom they share many genes. This situation is known as ***inbreeding***, a problem we have already alluded to in this chapter. Inbreeding can be defined as *the production of offspring related by descent*. To make our understanding more precise, consider three different biological meanings of inbreeding in terms of its measurement. A population's level of inbreeding can be assessed by: (1) a measure of shared ancestry in the maternal and paternal lineages of an individual; (2) a measure of genetic drift in a finite population; or (3) a measure of a system of mating in a reproducing population. Each of these three dimensions of inbreeding grows stronger in its effects as population size declines, and such effects can and must be measured to make informed and appropriate management decisions regarding breeding strategies for small populations (Templeton and Read 1994).

The first concept of inbreeding, the measure of shared ancestry of an individual in its maternal and paternal lines, has been called "inbreeding by descent" or ***pedigree inbreeding*** (Templeton and Read 1994). This type of inbreeding is quantified as the ***inbreeding coefficient***, symbolized by F_p (pedigree inbreeding). The value of F_p, which varies from 0 to 1, can be calculated, as we will do in a subsequent section, only for an individual of known pedigree. It measures the amount of ancestry an individual shares with its maternal and paternal lines. Pedigree inbreeding intensifies as the size of a population decreases.

The second concept of inbreeding is that of inbreeding as a measure of genetic drift in a population. If we knew the individual values of F_p for every individual in a population, added these values together, and divided the sum by the number of individuals, the resulting quotient would be the average probability of inbreeding by descent, symbolized as F_d. Here the subscript "*d*" is meant to signify that this value of *F* is a measure of the averaged inbreeding by descent of all members of the local population, or deme (Templeton and Read 1994). This value represents the average probability of inbreeding-by-descent, a measure of the effect of genetic drift on a population relative to an "ideal" population experiencing completely random mating.

Remember that the first type of inbreeding, pedigree inbreeding, increased in magnitude as population size declined. In the second type of inbreeding, inbreeding by descent, the value of F_d also increases as population size decreases and, for a given population size, F_d increases over time. This is expressed by the relationship

$$F_{d(t)} = 1 - [1 - 1/2N]^t,$$

where *t* is equal to time in generations. Note that the larger *t* becomes, the closer $F_{d(t)}$ comes to 1 (a completely inbred population). Thus, $F_{d(t)}$ will eventually reach a value of 1, and how fast it does so is a function of population size (Figure 6.7). The smaller the population, the faster it will become inbred. In this scenario, genetic drift causes the average probability of inbreeding by descent to increase and genetic variation to decrease. This means that inbreeding and loss of genetic variation are *correlates*, but inbreeding of this type is not the *cause* of a loss of genetic variation.

Finally, inbreeding can be used as a measure of a system of mating in a population, quantified as a value called the ***panmictic index***, *f*. The panmictic index measures inbreeding as a deviation from a reference population, which has a system of mating in which alleles at a locus are paired in proportion to their frequencies in the overall population (by definition, random mating). The panmictic index thus evaluates deviations from the heterozygosity frequencies expected under random mating, so

$$f = 1 - H_o / H_e,$$

where H_e is, as defined earlier, the expected heterozygosity under random mating and H_o is the observed heterozygosity. Recall that in a randomly mating population, the frequency of heterozygosity is defined by the Hardy-Weinburg equation. For two alleles, *p* and *q*, that frequency is

$$(p+q)^2 = p^2 + 2pq + q^2.$$

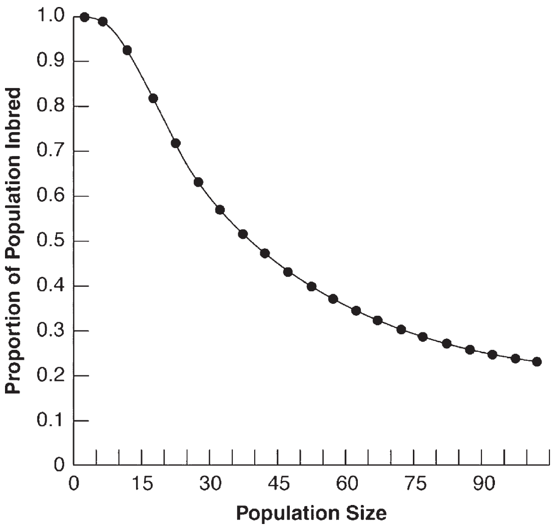


FIGURE 6.7. The relationship between the proportion of inbred individuals in a population and population size. The smaller the population, the less time it will take to become completely inbred. (Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

Thus, the expected frequency of the heterozygote is $2pq$. For example, if the frequency of allele p is 0.6 and the frequency of allele q is 0.4, then the H_e is $2 \times 0.6 \times 0.4 = 0.48$. Observed heterozygosity (H_o) can be calculated from genetic measurements of sampled individuals. If observed heterozygosity is greater than expected, $f < 0$, and the population has a reproductive system that avoids inbreeding. If observed heterozygosity is less than expected, $f > 0$, and inbreeding is not avoided. The value of the panmictic index can be used to quantify the degree of avoidance of inbreeding in a population.

Measuring these three aspects of inbreeding separately and accurately provides a powerful array of information from which to make intelligent management decisions for any population, but these measurements can be especially important in managing breeding in a captive population. Using the values of F_p in a captive breeding program, for example, a manager can determine which potential breeding pairs would produce inbred versus non-inbred offspring. If the goal is to minimize inbreeding, a manager could choose to mate individuals who are least related to one another, thereby avoiding the production of inbred offspring. An animal which is itself inbred should not be excluded from the breeding pool, but breeding pairs should be selected to avoid the creation of inbred offspring. Using the value of F_d, a manager could determine the effect of genetic drift on a population and the degree of heterozygosity present in that population and, from these data, make an intelligent decision about whether the current population size is sufficient to maintain an acceptable level of heterozygosity. Using the value of f, a manager could determine if current mating systems in the population lead to avoidance or encouragement of inbreeding, and then act accordingly.

6.4.2. The Problem of Inbreeding Depression

When populations become inbred, genotypic frequencies are skewed toward increased proportions of homozygous individuals and heterozygosity declines. As the proportion of homozygous individuals increases, so will the manifestation of recessive traits, which can only be expressed in a homozygous condition, but which are maintained in the population by heterozygous carriers. In environments that select against recessives, inbreeding can then lead predictably to *inbreeding depression*.

Inbreeding depression, as noted earlier, is a pattern of reduced reproduction and survival that occurs on account of inbreeding (Frankham et al. 2002:24), and can happen when historically large, outcrossing populations suddenly decline to only a few individuals. These remaining individuals may or may not be related. However, with the limited mate choices now available to them, high average relatedness will result in just a few generations. The population then experiences reduced survival and fecundity. As mate choice is now restricted to related individuals, inbreeding depression may increase as relatedness increases (Figure 6.8). When the degree of relatedness of individuals in the population ("inbreeding by descent") is regressed against one or more traits affecting fecundity or survival, the resulting regression can be used to calculate the degree to which increased mortality or lower fecundity is associated with increased relatedness.

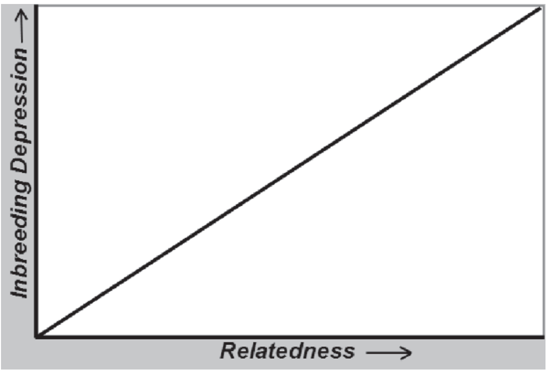


FIGURE 6.8. Relationship of relatedness in mating to levels of inbreeding depression, which is the decline in fitness (reduced survival and fecundity) associated with increased frequencies of mating among closely related individuals. The probability of an individual mating with a relation increases as the population size decreases. (Figure by M. J. Bigelow.)

Inbreeding depression is an especially well-documented problem in captive populations of vertebrates (Frankham 1995b). Forty-two of 45 captive, inbred vertebrate populations examined by Ralls and Ballou (1983) had reduced juvenile survival compared to outbreeding populations of the same species. The most comprehensive experimental studies of inbreeding have been conducted by conservation geneticist Richard Frankham and his colleagues. Using captive populations of the fruit fly, *Drosophila melanogaster*, Frankham created experimental populations in which he manipulated density, rates of inbreeding, and levels of environmental stress. In these experiments, several recurring trends appeared: (1) inbreeding and consequent loss of genetic diversity reduced the resistance of the flies to disease; (2) in inbred populations, extinction rates rose as the level of environmental stress was increased by adding additional stress factors (Figure 6.9); (3) the adaptive evolutionary potential (capacity for long-term genetic change) was reduced in small populations as environmental stress was increased; and (4) rates of inbreeding increased under stressful conditions (Reed et al. 2002; Frankham 2005). Among populations of deliberately inbred domestic animals and plants, up to 95% became extinct after eight generations of brother-sister matings (animals) or three generations of self-fertilization (plants) (Frankel and Soulé 1981). In wild populations,

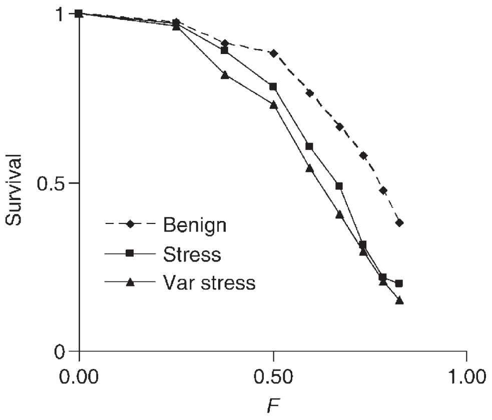


FIGURE 6.9. Proportion of populations of *Drosophila melanogaster* surviving at different inbreeding coefficients (F) for inbred (full-sib mating) populations in benign (no stress), single stress factor, and variable stress factor environments. (Frankham 2005. Stress and adaptation in conservation genetics. *Journal of Evolutionary Biology*. Copyright 2005 by Blackwell Publishing.)

inbreeding depression has been documented in fish, snails, lions, shrews, white-footed mice (*Peromyscus leucopus*), and plants (Frankham 1995a and references therein).

Some inbreeding occurs in all populations, no matter how large. However, inbreeding has disproportionately detrimental effects on small populations. Caughley (1994) provides a summary of the sequence of events that inbreeding can initiate:

1. The frequency of mating between close relatives rises
2. Heterozygosity is reduced in offspring, reducing the ability of the population to respond to environmental change
3. Semi-lethal recessive alleles are expressed in a homozygous condition
4. As a result of this expression, fecundity is reduced and mortality is increased
5. The population becomes even smaller, amplifying the sequence initiated in step 1

Caughley referred to this sequence as the "extinction vortex" of a positive feedback loop, or as Caughley put it, "the worse it gets, the worse it gets" (Caughley 1994). Thus, inbreeding can begin and sustain a pattern of significant decline in a small population.

6.4.3. Measures of Inbreeding

The most basic measure of inbreeding, as noted previously, is the inbreeding coefficient, F, which is a measure of the loss of heterozygosity in a population due to the effects of inbreeding. Therefore, one can estimate the inbreeding coefficient from changes in heterozygosity over time. Earlier, we defined the concepts associated with this measure, and now we will undertake its calculation. This measure of the inbreeding coefficient, known as the "effective inbreeding coefficient" (F_e) can be estimated as

$$F_e = 1 - (H_t / H_0),$$

where, as you recall, H_t is the level of heterozygosity at time or generation t and H_0 is the level of heterozygosity in the previous or base comparison generation. For example, if the level of heterozygosity in generation t is 0.4 and the level of heterozygosity in the previous generation *0* was 0.8, then the value of F_e is

$$1 - (0.4/0.8) = 1 - 0.5 = 0.5,$$

which means that inbreeding has reduced heterozygosity over this period of time in this population by 50%. One also can use the same relationship to make comparisons between related populations. For example, suppose the levels of heterozygosity of a small island population of individuals and that of the larger mainland population they originated from, are both known and are respectively $H_{island} = 0.35$ and $H_{mainland} = 0.81$. Then the effective inbreeding coefficient indirectly estimated from these values is

$$F_e = 1 - (0.35/0.81) = 1 - 0.43 = 0.57.$$

We would thus conclude that inbreeding within the smaller island population has reduced its heterozygosity by 57% compared to the mainland population.

Alternatively, some effects of inbreeding can be evaluated by measuring the rate of juvenile survival, which is calculated theoretically as

$$\ln(S) = A + BF$$

where S is the juvenile survival rate, A the instantaneous rate of juvenile mortality in progeny of unrelated parents, B the same rate when the line is completely inbred ($H = 0$) and F the inbreeding coefficient (Ralls et al. 1979). This equation can be expressed as the line $S = A - BF$. A can then be estimated if B is known, and vice versa (Caughley 1994).

If one knows the F coefficient and a measure of the individuals' fitness in the population, it is possible to estimate the severity of inbreeding depression. A general measure of inbreeding depression is normally designated by the symbol δ, which represents the proportionate decline in mean fitness due to a given amount of inbreeding. In general, the relationship could be expressed as

$$\delta = 1 - (\text{fitness of inbred offspring}/\text{fitness of outbred offspring}).$$

However, to be useful, we must make the measurement more specific. For example, let us replace "fitness" in the above equation with "survival rate." Conventionally, the magnitude of inbreeding depression is expressed as the average reduction in mean fitness value per 10% increase in the F coefficient (Van Oosterhout et al. 2000). Given this information, we could estimate the value of inbreeding depression as

$$1 - \left[\frac{\text{Survival rate at } F = 0.25}{\text{Survival rate at } F = 0.0}\right].$$

For example, suppose that the survival rate at $F_{0.25} = 0.2$ and at $F_{0.0} = 0.8$. Then the cost of inbreeding is $1-(0.2/0.8)$ or $1 - 0.25 = 0.75$. Conceptually, the cost of inbreeding is the proportional decline in survival that can be attributed to inbreeding of a given magnitude. Such declines are well documented. In 38 species of mammals, Ralls et al. (1988) estimated the actual average cost of inbreeding to be 0.33.

The estimates we have examined so far are applicable to populations in which all individuals can be considered a single population unit. What would happen to the genetics of a population that was *both* small and subdivided? To answer that question, and explore another important dimension of inbreeding effects, we need to add one more theoretical component to our understanding of conservation genetics. That component is the concept of gene flow and metapopulation structure.

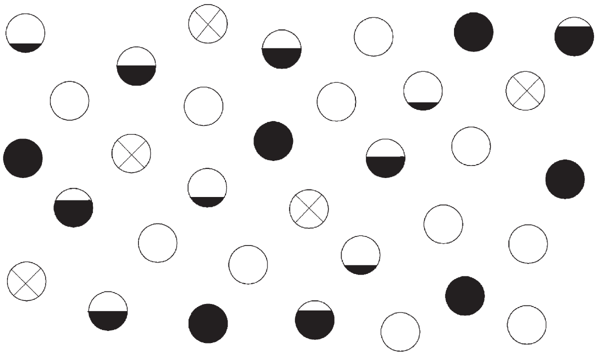


FIGURE 6.10. Diagrammatic representation of an arrangement of local populations of the same species (a "metapopulation"). Empty circles represent favorable habitats that populations do not occupy. Partially or completely filled circles represent favorable habitats and relative densities of populations in them as a proportion of the habitat's maximum capacity. Crosses indicate habitats in which local populations recently became extinct. (Adapted from Andrewartha and Birch 1954. Illustration by M. J. Bigelow.)

6.5. Inbreeding and Outbreeding in Population Subunits: Estimation of Gene Flow and Metapopulation Genetics

6.5.1. Historical Development of Gene Flow Theory

In 1954, the Australian ecologists H. G. Andrewartha and L. C. Birch noted that "A natural population occupying any considerable area will be made up of a number of … local populations or colonies" (Andrewartha and Birch 1954:657). This is perhaps the first published expression of the idea of a ***metapopulation***, a concept that Andrewartha and Birch represented clearly with elegant illustrations remarkably similar to those used in metapopulation literature today (Figure 6.10). However it was not until the late 1960s and early 1970s that the idea of metapopulations became an explicit model in population biology (den Boer 1968; Levins 1968, 1969, 1970). Levins offered perhaps the first intentional definition of a metapopulation as *any real population [that] is a population of local populations which are established by colonists, survive for a while, send out migrants, and eventually disappear* (Levins 1970).

Spatial subdivision affects the genetic structure of populations, and can influence the persistence of such populations in a landscape. Before the articulation of the concept of spatially divided populations by Andrewartha and Birch, a genetic basis for the same concept had been proposed by geneticist Sewall Wright in the 1930s (Wright 1931). Wright proposed a "shifting balance theory" of natural selection in which small, subdivided populations (demes) achieved high levels of local adaptation to changing environments through (local) natural selection, genetic drift, migration (among subunits), and interdemic selection (i.e., local extinctions of less-fit demes and colonization of new or vacated areas by more fit demes). The problem that Wright was attempting to solve was how novelty arose in a constantly changing environment. The small, subdivided populations served as "nature's many small experiments" (Wade and Goodnight 1998), and speciation resulted as a by-product of local adaptation when it produced reproductive isolating mechanisms. It was this subdivision that prevented the averaging of environmental variation into a single genetic optimum ("one size fits all") for the entire population. Thus, genetic optima shifted in different population subunits.

Historically, the scientific alternative to Wright's shifting balance theory was R. A. Fisher's theory of large population size (Fisher 1958), which was an attempt to explain how existing adaptations were refined in a slowly changing environment (Wade and Goodnight 1998; Table 6.5). Fisher saw the world as a collection of large, interbreeding (panmictic) populations in which adaptation occurred primarily through mutation and natural selection. Genetic drift and migration were at best inconsequential, and at worst counter-productive to adaptation. In contrast, Wright saw genetically subdivided populations of multiple and varied fitness peaks, Fisher envisioned "fitness" as a global average for the entire population.

Although both theories found support, the weight of opinion traditionally favored Fisher's theory as the simpler explanation for empirical data from natural populations, which were assumed to be panmictic. If populations had apparent separation and spatial diversity, they still faced no real barriers to migration, exchange, or gene flow. However, by the 1960s, the realities of habitat destruction and fragmentation, combined with increasing concern over growing rates of species' extinctions, led researchers to

Table 6.5. Essential differences between Wright's Shifting Balance Theory and Fisher's Theory of Large Population Size. Wright's Shifting Balance Theory provides a conceptual basis for understanding how metapopulation structure (spatial division of population subunits) might affect genetic and evolutionary change in a spatially divided population.

	Wright	Fisher
Central problem of evolutionary theory	Origin of adaptive novelty in a constantly changing environment	Refinement of existing adaptation in a stable or slowly changing environment
Major processes of evolutionary change	Combination of local natural selection, random genetic drift, migration, and interdemic selection	Mutation and natural selection
Ecological context of evolution	Small, subdivided populations	Large, panmictic populations
Genetic basis of evolutionary change	Epistasis and pleiotropy; context-dependence of allelic effects	Additive genetic effects; context-independence of allelic effects
Process of speciation	Inevitable by-product of local adaptation in epistatic systems	Disruptive or locally divergent selection

Source: Wade and Goodnight (1998). Perspective: the theories of Fisher and Wright in the context of metapopulations: when nature does many small experiments. *Evolution*. Copyright 1998 by Blackwell Publishing.

question the generality of contiguously distributed, panmictic populations.

Wright's shifting balance theory has profound implications for the maintenance of biodiversity as well as for the dynamics of metapopulations. Wright proposed that evolution might proceed rapidly in spatially structured populations, especially if local extinctions and re-colonizations occurred (Hanski and Simberloff 1997). Wade and Goodnight (1998) note that "Wright imagined that the membership of most species was distributed into small, semi-isolated breeding groups." In such a system, random genetic drift and selection within demes become strong evolutionary forces. Far from being detrimental to the population, random genetic drift and ***epistasis*** become potential sources of additional genetic variance by fueling additional adaptation to local conditions within metapopulations (Wade and Goodnight 1998) and potentially could create more genetic variance per generation than mutation (Wade 1996). Wright's Shifting Balance Theory also made the processes of gene flow, migration, and recolonization of temporarily vacant habitats essential to understanding genetic change in populations. We now take up the study of these processes, and their effects on population genetics, in greater detail.

6.5.2. Current Models of Gene Flow: Predictions and Implications

Gene flow, previously discussed in Chapter 4, is the movement of genes between populations or population subdivisions and can be determined from the expression

$$N_e m = \frac{1 - F_{ST}}{4F_{ST}}$$

where N_e is the effective population size, m is the rate of immigration and F_{ST} is the total genetic diversity found among all populations. The result is expressed in immigrants per generation. But how do genes really get from here to there in natural populations, and how will this affect the actual genetic diversity of these populations? Three models of gene flow have been proposed to provide a conceptual understanding of the process and its effects on genetic diversity.

Traditionally, ecologists have believed that populations, and the genes they carried, tended to move or disperse a single step among population subunits each generation. This view, known as the ***Stepping-stone Model***, would mean it would take many generations for an introduced allele to move through all segments of a large population (Figure 6.11A). Wright argued, in contrast, that gene flow would be equal and constant among all subdivisions in a population. We can visualize Wright's model as one in which new alleles come from a single source (mainland) and move to all new areas (islands) at the same time. Hence it is often referred to as the "Mainland–Island Model" or simply as the "Island Model" (Figure 6.11B) A third, more recently developed view is that the probability of an allele from one source point decreases with distance to potential destination points, and the so-called "Isolation-by-distance" Model (Figure 6.11C). Thus, in comparative terms, the Stepping-stone Model would predict the slowest rates of gene flow, the Island Model the highest, and the Isolation-by-distance Model intermediate (and highly variable) rates (Hamrick and Nason 1996:205–206).

A reasonable assumption of all three models is that genetic heterogeneity among populations should be solely a function of gene flow (i.e. you can't have shared genes unless you exchange individuals). As part of the development of his Shifting Balance Theory of population genetics, Wright developed three measures, often referred to as "Wrights' F statistics," for measuring and partitioning genetic variation within and among individuals of a population that was subdivided into separate genetic units, a necessary part of his theory's elaboration if one were to understand how spatially subdivided populations were structured genetically. The first, known as Wright's F_{ST}, is a measure of the correlation of genes of individuals within subpopulations or, more precisely, the proportion of the total genetic

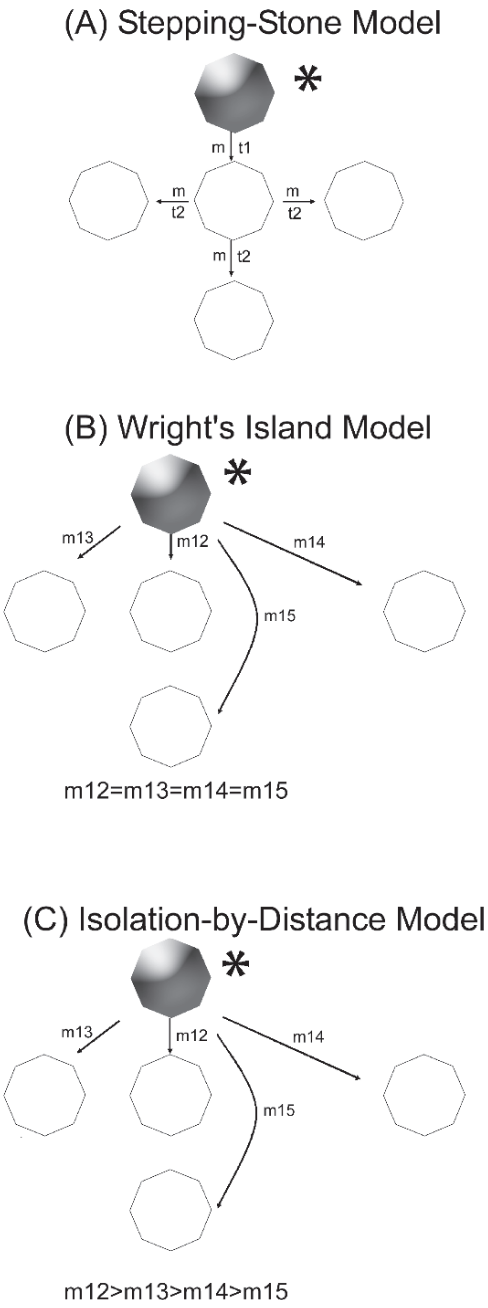


FIGURE 6.11. Three models of gene flow in populations of a single species spatially separated from one another (metapopulation). In each model a novel allele (*) is assumed to be initially introduced into one population. In the Stepping-stone model (A), gene movement (*m*) is in a given generation (*t*) is only among adjacent, evenly-spaced populations. In Wright's Island model (B), the rate of gene movement in any given generation is equal among all populations regardless of spatial location. In the Isolation-by-distance model (C), gene flow rates are a function of distance, with gene flow being higher among neighboring populations and lower among populations more remote from one another. (After Hamrick and Nason 1996. Illustration by M. J. Bigelow.)

variation of the population that is found among subpopulations within individuals. The second statistic, known as Wright's F_{IS}, is a measure of the correlation of genes within individuals relative to the gene frequencies within the subpopulation, in other words, a measure of subpopulation genetic variability. Finally, Wright's F_{IT} reflects the correlation of genes within individuals relative to gene frequencies of the entire population. The three measures can be quantified as

$$F_{ST} = (\theta - \alpha)/(1 - \alpha)$$

$$F_{IS} = (F - \alpha)/(1 - \theta)$$

$$F_{IT} = (F - \alpha)/(1 - \alpha)$$

where θ is the correlation of genes between randomly selected individuals in the same subpopulations, α is the correlation of genes between random individuals from different subpopulations, and F is the correlation of genes within individuals (Chesser et al. 1996).

Wright's F statistics are used to determine the breeding structure of populations (i.e. was genetic variation randomly distributed in subunits, or were subunits genetically different from population means?) and to determine indirect indices of dispersal among subunits. The second use is based on that fact that, the more closely the genetic characteristics of subunits match average genetic population characteristics, the more exchange of genes (gene flow) must be taking place between the subunits. Wright's ideas have been easily incorporated into models and theories of metapopulations and their genetics, such that we can restate the value of Wright's F_{ST} more simply. Treating the genetic subunits as subpopulations of a metapopulation, we can compare a familiar genetic measure, heterozygosity, H, within population subunits, H_s, to the average heterozygosity of the total metapopulation, H_T, and rewrite Wright's F_{ST} expression as

$$F_{ST} = \frac{H_T - H_s}{H_T},$$

which tells us the ratio of *between subunit heterozygosity* to *total metapopulation heterozygosity*, a measure of genetic diversity among subpopulations.

Although we have already examined one expression of gene flow as a measure of "immigrants per generation," a more genetically precise and widely used measure is Nei's G_{ST} (Nei 1972), which is the proportion of total genetic diversity in a population attributable to differentiation among subpopulations. In other words, Nei's G_{ST} is simply a multi-allelic equivalent of Wright's F_{ST} (Hamrick and Nason 1996:207). The value of G_{ST} can be determined if we can measure the total genetic diversity of the population at a given locus (total heterozygosity or H_T) and partition it into genetic diversity within populations and among populations. The ratio of the among-population component of diversity (D_{ST}) to the total diversity is a measure of gene flow, or Nei's G_{ST}, expressed as

$$G_{ST} = \frac{D_{ST}}{H_T}$$

The model of dispersal will affect the value of G_{ST}. The Stepping-stone Model, with its low rates of gene flow, should show the greatest differences between population subunits (highest G_{ST}). The high levels of gene flow predicted by the Island Model should more thoroughly "mix" the genetics of the population and produce a low value of G_{ST}.

6.5.3. Models of Recolonization: Propagule Pools and Migrant Pools

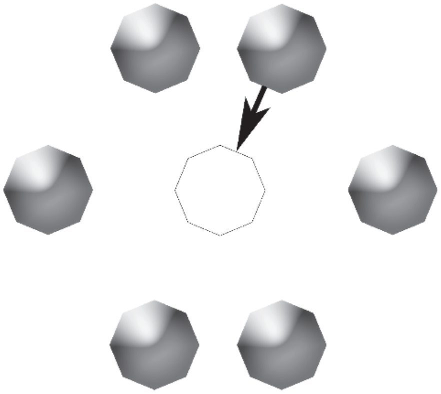
In nature, populations do suffer local extinction, often to be recolonized later from other sources. As with the more general models of dispersal, the degree of subunit differentiation and associated value of G_{ST} will affected by the pattern of recolonization (Figure 6.12). The patterns of recurrent local extinctions and recolonizations characteristic of metapopulations significantly affect the genetic structure within and among local population subunits (demes), and additional genetic models of metapopulations have been formulated to explain and predict the intricacies of metapopulation genetics.

The nature of the genetic effect depends upon specific recolonization patterns. The "Propagule-Pool" Model (Figure 6.12A) is a genetic analogy to the previously discussed Mainland-Island Model of metapopulations because it assumes that all colonists are drawn from a single extant deme in the metapopulation. In Propagule-Pool Model of recolonization, the vacant habitat associated with a local extinction is recolonized by individuals (propagules) that all come from the same subunit (pool).

In contrast to the Propagule-Pool Model of gene flow in metapopulations, the "Migrant-Pool" Model assumes that colonists to a new deme are drawn randomly from the entire metapopulation (Slatkin 1977) (Figure 6.12B). In both models, local extinctions cause decreases in the genetic diversity of the metapopulation, both within and among demes, but genetic diversity is maintained at higher levels in the Migrant-Pool Model (Pannell and Charlesworth 1999). Such higher levels of diversity occur because sites colonized by individuals from different demes approximate the genetic diversity of the entire metapopulation, rather than the genetic diversity of only one deme.

We will not work out the details of the mathematical relationships here (Wade and McCauley 1988), but we will examine the general trends and implications of these two models for changes in population genetic structure. Specifically, if the Propagule-Pool Model is a recurrent pattern, recolonized subunits will each have unique genetic traits heavily influenced by their founders (the original propagules), and their genetic differentiation (G_{ST}), compared to the overall population, will be greater. In contrast, the Migrant-Pool Model assumes that colonists for vacant habitat are recruited randomly from many pools. In this scenario, genetics of the new population subunit are representative and may not be differentiated from other subunits if the number of colonists is large relative to the number of migrants in the population (Wade and McCauley 1988). If the number of colonists is small, colonists are less likely to be representative of the population and the predicted value of G_{ST} will be higher.

(A) Propagule-Pool Model



(B) Migrant-Pool Model

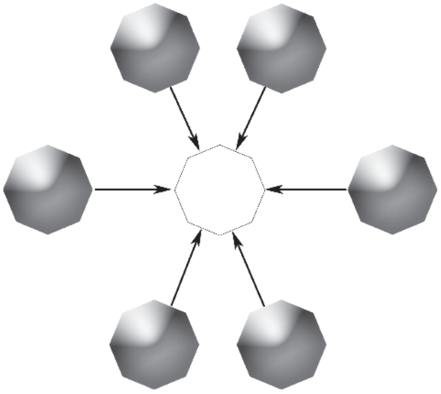


FIGURE 6.12. Two models of extinction and recolonization in spatially separated populations of the same species. The open circle represents a site occupied by a population that has recently become extinct. In the Propagule-Pool model (A), colonists to the vacant site are recruited from a single extant population, resulting in more genetic differentiation among populations (increasing G_{ST}). In the Migrant-Pool model (B), colonists are recruited randomly from all populations. As a result of recolonization by this random sample, genetic differentiation may increase or decrease. If the number of colonists is large relative to the number of migrants, G_{ST} will decline, but if the number of colonists is small relative to the number of migrants, G_{ST} will increase. After Hamrich and Nason 1996:209. Illustration by M. J. Bigelow.

The predictions of these models have been supported by studies of real metapopulations, reinforcing the assumption that genetic diversity within and among demes is influenced by characteristics and methods of dispersal, as well as distances between populations. Undersea hydrothermal vents offer a classic metapopulation example. The vents are highly specialized, discrete, patchily distributed, and surrounded by non-habitat of more typical ocean floor. Deep-sea invertebrates often disperse along rifts in the ocean floor where vent activity is prominent. Vrijenhoek (1994) found that indices of gene flow and genetic differentiation declined with increasing distance between populations in some species that had poor dispersive abilities, such as the giant tube worm (*Riftia pachyptila*) (Figure 6.13), a result consistent with the Isolation-by-distance Model of gene flow previously described. Distance had less effect on species with greater dispersive abilities, such as the mussel *Bathymodiolus thermophilus*, whose mobile larvae disperse widely via ocean currents.

These models also have implications regarding the effect of habitat fragmentation. If a population has relatively little differentiation between subunits (low genetic structure), fragmentation is unlikely to result in significant loss of genetic diversity because each subunit is reasonably representative of the entire population (Figure 6.14A). If, on the other hand, a population has a high level of differentiation between subunits (high genetic structure), then there is the potential for significant loss of population genetic diversity (Figure 6.14B). Conservation geneticists James Hamrick and John Nason note a further dimension of these implications. “As a result of the expected loss of genetic diversity, the tendency is to abandon fragments as being of little value. This may be a mistake, because fragments, if maintained and preserved, can serve as reservoirs of genetic diversity” (Hamrick and Nason 1996:228).

FIGURE 6.13. A colony of giant tubeworms (*Riftia pachyptila*), denizens of deep-sea hydrothermal vents and a species with poor dispersive abilities. Genetic differentiation (G_{ST}) between populations is high and increases with distance, supporting the Isolation-by-Distance Model of genetics in metapopulations. The genetic structure of mussel populations, represented by some individuals around the tubeworms, will be less affected by distance between population subunits because of their highly mobile larvae. (Photo courtesy of Karen Von Damm.)

Although such models are useful in making predictions in field experiments, real populations also are influenced by the type of breeding system employed, especially in plants, where breeding systems strongly influence dispersal distances and genetic exchange. Hamrick and Godt (1989) demonstrated that, both within species and within populations, outcrossing plant populations usually had higher levels of polymorphic loci, a larger number

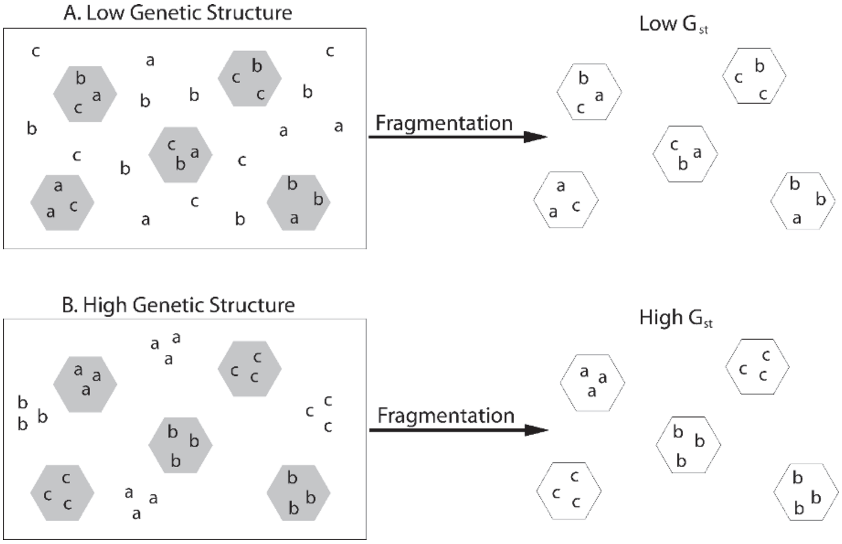


FIGURE 6.14. The effect of habitat fragmentation on maintenance of genetic diversity in a metapopulation. Under conditions of low genetic structure (A), there is little loss of genetic variation following fragmentation because resulting populations in the fragments are random samples of the population’s original genetic diversity, and there is little genetic differentiation (low G_{ST}) among fragments. If a population has high genetic structure (B) (populations in different parts of the original habitat are genetically different), fragmentation can result in greater differentiation of remaining fragmented populations (high G_{ST}), with concurrent loss of genetic diversity because lost habitat contained genetically unique populations. (After Hamrick and Nason 1996. Illustration by M. J. Bigelow.)

of alleles at each polymorphic locus, and higher levels of heterozygosity than selfing plant populations, and wind pollinated species tended to be higher in all these measures of genetic diversity than animal pollinated species (Hamrick and Godt 1989).

In both individual population units and metapopulations, geneticists today emphasize the dangers associated with inbreeding (Frankham 1995a), but some conservation biologists have asserted that genetic concerns in small populations are of less importance than historically believed and that "… loss of diversity is more likely to be a symptom of endangerment than its cause …" (Holsinger et al. 1999). As Holsinger et al. (1999) put it, "… those alleles most likely to be lost as a result of genetic drift – rare alleles – are also the least likely to contribute to any immediate response to natural selection." Further, there are some small populations that show excellent long-term viability with no sign of negative genetic effects (Simberloff 1988; Walter 1990), and thus cast doubt on the assertion that inbreeding is always detrimental to population persistence and viability. In fact, some wild populations are notoriously inbred, yet persistent, such as the blue duck (*Hymenolaimus malacorhynchos*), an endemic species of New Zealand, whose inbreeding seems to be a product of its isolated populations and low dispersal abilities (Triggs et al. 1992). As more studies are completed, the effects of inbreeding depression have become the subject of intense debate. The critical question is: can we identify any specific cases in the wild, in populations or population subunits, in which inbreeding is the identifiable causative factor in extinction? This is a critical question for assessing the relevance of conservation genetics to conservation biology. We will examine the question in detail, learning what we can from captive and laboratory populations, theoretical models of populations, and natural populations themselves.

6.6. Can Inbreeding Cause Extinction?

6.6.1. Laboratory Experiments and Models

In laboratory experiments on inbreeding in the fruit fly, geneticist Richard Frankham and his colleagues have been able to demonstrate that inbreeding and associated loss of genetic variation (1) reduced resistance to disease, (2) led to increased extinction rates in environmentally stressed populations, and (3) reduced adaptive evolutionary potential (heritability) in small populations subjected to stressful environments (Frankham 2005). Further, Frankham's studies demonstrated that, when populations were subjected to environmental stress, rates of inbreeding increased.

In a controlled experiment involving both field and laboratory environments, Jiménez et al. (1994) estimated the survivorship of inbred and non-inbred white-footed mice in a mixed deciduous forest in Illinois (USA). Mice in both treatments had been raised in a laboratory but were all descendents of wild mice. Mice were released into the field and recaptured at regular intervals, and trapping was done on surrounding adjacent habitat to estimate the proportions of mice that left the release site. Most mice were captured within 50 m of their release sites, and emigration rates were not different in the two treatments. Based on release–recapture ratios of marked mice in both inbred and non-bred treatments, Jimenez et al. determined that, over a 10-week period, non-inbred mice had consistently higher survivorship than non-inbred mice (Figure 6.15). Some differences were sex-specific. For example, male mice in both treatments lost weight in the first few days after release. Non-inbred males regained their weight loss, but inbred males continued to lose weight throughout the experiment. Overall, a recent analysis of 33 population data sets revealed that approximately 40% of the variation in fitness in these populations could be explained by variance in heterozygosity, which is a reliable index of inbreeding (Reed and Frankham 2001).

Low survivorship is one explanatory factor in extinction, and there is a clear threshold relationship between rates of inbreeding and rates of extinction in many species, with increasing rates of extinction beginning at intermediate levels of inbreeding (Frankham 1995b). In one model, Frankham (1995b) demonstrated that changes in the inbreeding coefficient (F) produced little change in survivorship (S). Figure 6.16 depicts this relationship by comparing the value of the inbreeding coefficient to the

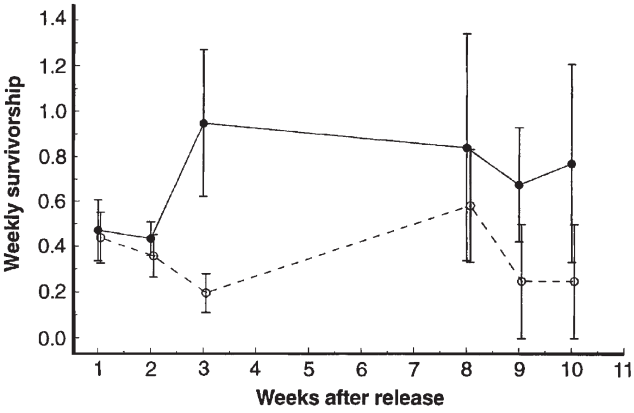


FIGURE 6.15. Survivorship of inbred (dotted line) and non-inbred (solid line) white-footed mice (*Peromyscus leucopus*) in a mixed deciduous forest in Illinois (USA). Bars represent standard errors of estimates. Non-inbred animals had higher survivorship than inbred animals in all time intervals. Although none of the differences between groups are significant for any one estimate, when the estimates are used as repeated measures of survivorship for groups the difference is statistically significant. (Jiménez et al. 1994. An experimental study of inbreeding depression in a natural habitat. *Science* 266:271–273. Reprinted with permission from AAAS.)

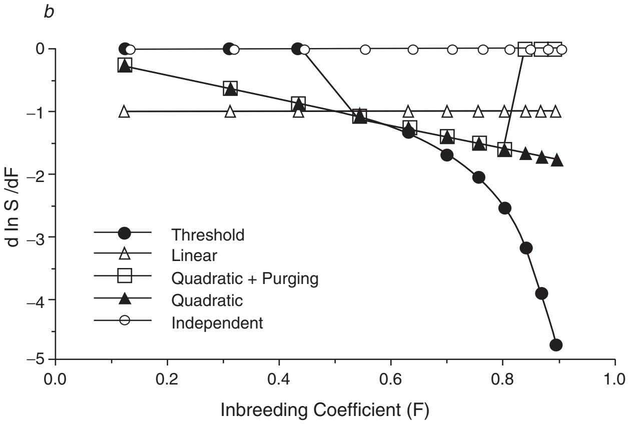


FIGURE 6.16. The threshold effect of inbreeding on fitness. This model suggests that inbreeding has little effect at very low levels, but begins to cause an increasing rate of decline in fitness, indexed by changes in survivorship (*S*), when it passes a "threshold" level of about $F > 0.45$. (Frankham 2005. Stress and adaptation in conservation genetics. *Journal of Evolutionary Biology*. Copyright 2005 by Blackwell Publishing.)

ratio of the change in the natural log of survivorship (d ln*S*) over change in the inbreeding coefficient. Note that when the value of *F* is relatively low (0.00–0.45), increases in *F* produce almost no changes in survivorship (the slope of the line is near zero). But when the inbreeding coefficient passes a critical "threshold" level (here, above about 0.45) survivorship declines rapidly with even small increases in *F*. Frankham's model demonstrates that high levels of inbreeding lower survivorship, but even low rates of inbreeding have been associated with extinction at fixed, finite population sizes (Latter et al. 1995).

Frankham's models would lead us to predict that inbreeding should be inversely correlated with fitness in any population. Taking matters a step beyond model predictions, Van Oosterhout et al. executed a carefully designed laboratory experiment on the squinting bush brown butterfly (*Bicyclus anynana*) in which they manipulated levels of inbreeding, gene flow, and population size in different populations (Van Oosterhout et al. 2000) while measuring various fitness components in each group. One key fitness metric, lifetime female fecundity, was inversely proportional to the inbreeding coefficient of the female parent (Van Oosterhout et al. 2000). Smaller and more inbred populations also had more sterile egg clutches. Other key fitness indices such as zygote mortality, juvenile mortality, adult male and female longevity, and male development all were detrimentally affected by inbreeding (Van Oosterhout et al. 2000).

6.6.2. Field Studies of Inbreeding

In addition to other effects, inbreeding increases the impact of genetic drift, which is likely to further reduce a population's genetic variability (Templeton and Read 1994). Aside from increased mortality and decreased fecundity associated with inbreeding depression, inbreeding also appears to affect the genetic structure of populations. For example, Sullivan (1996) found that among populations of Colorado chipmunks (*Tamias quadrivittatus*) in the southwestern United States, inbreeding depression was more serious in relict and isolated populations with limited gene flow, even if the overall population was large and geographically widespread. The most isolated populations had little or no genetic variation at up to 30 loci (Sullivan 1996).

Although this knowledge of chipmunk genetics is interesting, a conservation biologist concerned with the pressing question of extinction might be justified, if not entirely polite, in asking, "So what? Are these isolated chipmunk populations really in any danger because of inbreeding?" A dramatic answer to this question was provided, in part, by a serendipitous natural experiment on Mandarte Island, off the coast of British Columbia, Canada. Here, a long-term research effort on song sparrows (*Melospiza melodia*) had been marking individuals over several generations, such that an extensive amount of population demographics had been determined, including the inbreeding coefficients of most individuals. The population crashed in 1989, with 206 dying and only 10 surviving. Every sparrow with an inbreeding coefficient of 0.0625 or higher died. In contrast, the ten survivors had an average inbreeding coefficient of only 0.0065, and only three of these had known inbreeding (Keller et al. 1994).

In this population of song sparrows, the evidence suggests that natural selection favored outbred individuals during a period of environmental stress, and conceivably the population could have perished if no non-inbred individuals had been present. Plant studies can answer the question of whether inbreeding can cause extinction even more definitively because inbreeding can, in some cases, lead to total reproductive failure. Some plant populations are *self-incompatible*, having individuals that are unable to generate viable seed production when they receive their own pollen. When inbreeding levels are high, plants in such populations may not recognize pollen from other individuals as "different," and reproduction fails. For example, in the rare lakeside daisy (*Hymenoxys acaulis*), native to shoreline areas of the southern portions of the Great Lakes in the US, the Illinois population was reduced to a small number of individuals that failed to set seed for 15 years. Researchers found that all individuals in the population were members of a single compatibility type, so pollen produced by one plant could not fertilize any other plant in the same population. The introduction of plants from an Ohio population may enable the daisy to persist in Illinois, but only at the cost of the loss of the genetically unique Illinois group (Holsinger et al. 1999). These problems can be exacerbated in any population that becomes fragmented and isolated. In another rare, self-incompatible daisy species, the button winklewort (*Rutidosis leptorrhynchoides*) of southeastern Australia, researchers found that small populations of less than ten plants showed increased likelihood of producing full-sib matings and families, but so did medium-sized populations of 100–200 plants that were isolated by more than 5 km from their nearest neighboring population (Young and Brown 1999). Such full-sib matings foreshadow the possibility of future inbreeding effects in these populations.

Some self-compatible plants show no reduction in reproductive output even when inbred. For example, Groom (1998) compared numbers of seeds produced by self-pollinated and out-crossed individuals of the annual herb *Clarkia concinna concinna*, (Santa Clara red ribbons), a species endemic to the northern coastal range of California. In this self-compatible plant, there was no difference in seed production between self-pollinated and outcrossed individuals within or among patches.

Generally, a variety of studies show that inbreeding is almost always likely to contribute to overall population decline, especially in species with low reproductive rates (Mills and Smouse 1994), and appears to universally reduce fitness in any population in which it occurs (Hedrick and Kalinowski 2000). But, in animal populations, our question is still not conclusively answered. Can inbreeding cause population extinction?

6.6.3. Inbreeding was a Cause of Extinction in Butterfly Populations

Inbreeding is more difficult to study in wild populations of animals, so its potential for causing extinction is more difficult to assess. But some assessments are possible. The most definitive results have come from the study of butterfly populations in Finland where Ilik Saccheri and his colleagues examined 42 population subunits (a metapopulation) of the Glanville fritillary butterfly (*Melitaea cinxia*) (Figure 6.17). This metapopulation, living on the Åland Islands off Finland's southwest coast, consists of numerous, small, more-or-less isolated populations that live in dry meadows on these islands (Saccheri et al. 1998). Individual population subunits are often transient, with overall turnover averaging 200 extinctions and 114 colonizations per year. Saccheri and his colleagues studied 42 population subunits of this species in this habitat from 1993–1995. They examined effects of area, past trends in population size, density of butterflies in the nearest neighboring populations, incidence of cattle grazing, and genetic heterozygosity on various measures of fitness, including larval survival, adult longevity, egg hatching rate, and risk of extinction of the population subunit. Heterozygosity is a potential and relative index of inbreeding, not a direct measure of it. Further, in this study, the measurement of heterozygosity used as the index of inbreeding was based on only seven polymorphic enzymes found on one microsatellite locus in the butterfly genome. Nevertheless, it is logical that heterozygosity and inbreeding should be directly related. As inbreeding increases, heterozygosity should decline. As Saccheri et al. stated "The variance in inbreeding among populations is expected to be high in this metapopulation, because there is substantial gene flow in many dense regional networks of local populations, but also close inbreeding in many local populations that are extremely small and quite isolated. Thus, differences in average heterozygosity of local populations, even if based on a limited number of polymorphic loci, should reflect real differences in the degree of inbreeding" (Saccheri et al. 1998:419).

FIGURE 6.17. The Glanville fritillary butterfly (*Melitaea cinxia*), a species in which inbreeding was a significant causative factor in extinctions of populations in southern Finland. (Photo courtesy of Dr. Tom Brereton, and Butterfly Conservation.)

As in Van Oosterhout's study, Saccheri et al. (1998) found that female lifespan, percent of eggs hatching (based on average group size after hatching), and larval weight (taken as an index of larval survival) were all positively correlated with increasing heterozygosity, indicating that more homozygous, and presumably more inbred females, had shorter lifespans, lower rates of hatching success, and smaller, less viable larva. But the difference between Saccheri's findings and Van Oosterhout's was that Saccheri et al. also documented the fate of each of the 42 population subunits. Seven subunits became extinct. Using data from a larger sample of 336 population subunits and excluding the other 42, Saccheri et al. constructed a model that predicted the likelihood of extinction using both ecological factors and heterozygosity. When applied to the 42 studied population subunits, the investigators found that risk of extinction was explained to some degree by ecological and habitat variables (such as the abundance of nectar flowers in the meadow), but heterozygosity also was an important factor, explaining 26% of the variation in extinction risk.

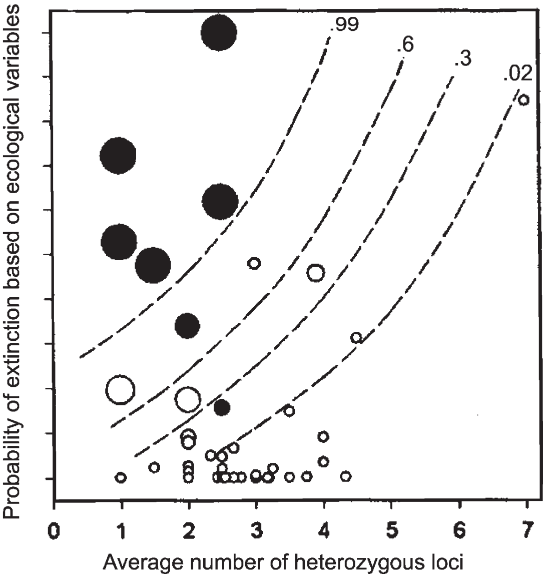


FIGURE 6.18. A model of extinction probability in metapopulation subunits of the Glanville fritillary butterfly (*Melitaea cinxia*) as explained by heterozyosity. Black circles represent subunits that became extinct, open circles populations that remained extant. Size of circle reflects visual representation of relative extinction probability. Dashed lines represent isoclines of equal extinction probabilities predicted by a model incorporating both heterozygosity and ecological variables. (Reprinted by permission from MacMillan Publishers Ltd. Saccheri et al. 1998. Inbreeding and extinction in a butterfly metapopulation. *Nature* 392:491–494. Copyright 1998.)

Note how dramatically the risk of extinction drops as the number of heterozygous loci increases (Figure 6.18).

6.6.4. Inbreeding Effects – Environmental and Demographic Variability

There have been cases in which scientists have hypothesized that inbreeding was the cause of population decline, only to discover upon investigation and analysis that it was not. A notable example of this sort occurred in studies of the black and white ruffed lemur (*Varecia variegata*) of Madagascar (Figure 6.19). From 1991 to 2001, family groups of these lemurs living in Madagascar's Manombo Special Reserve failed to produce a single offspring, but other groups studied outside the reserve did. Given that the Manombo population was small and fragmented within the reserve, inbreeding depression was immediately suspected as the culprit. To test this hypothesis, Edward Louis, Jr. and his colleagues examined blood samples of lemurs from the Manombo population and from three other populations outside the reserve which had produced offspring. All four populations showed evidence of inbreeding in higher than expected levels of homozygosity, attributable to population declines and bottlenecks experienced by all four populations. Although values of F_{ST} demonstrated that all populations were genetically distinct from one other, none were different from the overall mean in their levels of heterozygosity nor in their allelic diversity ($\bar{X} = 3.05$ alleles per locus). The Manombo population did not differ from other populations in estimates of inbreeding or in its level of relatedness of individuals to one another, nor in its genetic distinctiveness (measured by Nei's G_{ST} previously discussed) from other populations (Louis et al. 2005).

FIGURE 6.19. The black and white ruffed lemur, *Varecia variegata*, of Madagascar. Studies of this species show that, despite evidence of inbreeding, observed reproductive failure in individual populations in may be more likely attributable to nutritional deficiencies induced by environmental stochasticity. (Photo courtesy of E. E. Louis Jr.)

If inbreeding was the cause of reproductive failure in the Manombo population, such failure should have occurred in all four populations because all were inbred at similar levels, but this was not the case. There was a notable difference among populations in habitat quality, because a cyclone, which struck the island in 1997, destroyed a large portion of the fruit-producing trees that lemurs in Manombo Reserve relied upon as a food source. Louis et al. noted, regarding these results, that "The striking difference between the populations was not the level of genetic diversity, but rather the stochastic event that depleted the mature fruit trees from the Manombo Reserve. These trees supplied the primary nutritional plants for *Varecia* and their loss is likely to have impacted the nutritional status of the population. … Therefore, it seems probable that nutritional, rather than genetic, factors are responsible for the recent lack of reproductive success on the part of *V. variegata* at Manombo Special Reserve" (Louis et al. 2005:110).

We must recognize that the alternative explanation, destruction of food-producing trees, is itself an untested hypothesis, and does not explain the reproductive failure of the Manombo population from 1991 to 1996. What Louis et al. did demonstrate was that inbreeding probably was *not* the cause of reproductive failure. But if the proximate cause of reproductive failure was environmental stochasticity (the cyclone), then the observed reproductive failure is consistent with the predictions of previously described experiments by Frankham (2005) which showed that inbred populations were especially susceptible to environmental stress. Perhaps, when it comes to inbreeding, inbred lemurs are not so different from inbred fruit flies.

POINTS OF ENGAGEMENT – QUESTION 2

Describe the experiment you would design to determine if reproductive failure of the ruffed lemurs in Manombo Reserve is attributable to a nutritional deficiency caused or aggravated by the destruction of large fruit producing trees. What would be your research hypothesis, null hypothesis, and test consequence?

As in animals, inbreeding depression cannot be assumed to be the cause of reduced fitness or population decline in every inbred plant population. Pico et al. (2004) reviewed the effects of inbreeding in a variety of different genotypes in populations of the perennial herb Butterfly Blue (*Scabiosa columbaria*). In this species, there was high variance of inbreeding effects among different genotypes. Some showed strong effects of inbreeding depression, but about as many showed inbreeding enhancement (increased fitness when inbred), and a third category, containing a large number of families, showed no effects of inbreeding at all. The authors concluded that some inbred, selfing populations had fitness advantages to the extent that they could successfully invade and replace outcrossing populations (Pico et al. 2004). These results should not be used to dismiss the real dangers of inbreeding depression in threatened species and small populations, but they do indicate the need for many more species-specific and genotype-specific studies on the effects of inbreeding. Further, there is a need to not only study effects of inbreeding on small populations and threatened species, but also on common species, especially in plants.

6.7. Hybridization and Introgression

6.7.1. Hybridization and Introgression in Animals: The Case of the Red Wolf

Hybrids refer to individuals that are the offspring of matings between individuals of different species, subspecies, or populations. In animals, hybrids typically suffer a number of disadvantages compared to non-hybrid individuals. Animal hybrids may be infertile, or even if fertile, they may have reduced mating success because non-hybrid individuals in both their parental species may not recognize them as potential mates. These and related problems make ***hybridization*** in animals a waste of reproductive effort by the parent individuals, and wasted reproduction is not something individuals in small populations can afford. Thus, hybridization can be especially threatening to rare species due to reduced fitness of hybrids or through its destruction of unique genotypes of rare species (genetic assimilation). The problem is compounded because some conservation legislation, such as the US Endangered Species Act (ESA), offers no protection to hybrids. This means that hybrid animals could suffer two disadvantages: lower fitness and no legal protection.

These liabilities become significant when hybrids occur between rare species, or between a rare species and a more common species. That is, when two closely related species coexist, and one of them is very rare, the rare species may be genetically swamped, and its unique genome exterminated, by interbreeding and hybridization with the more common species. A related problem, ***introgression***, is a common result of hybridization. Introgression is the acquisition and incorporation of genetic material from one species, subspecies, or population into the genome of another. Introgression makes it difficult to identify, establish, and maintain the genetic integrity of a species in relation to other, closely related species. One of the best, and most complex, examples of problems that can arise from inbreeding, hybridization, and introgression involves the case of the red wolf (*Canis rufus*) of the south-central United States (Figure 6.20).

Attempts to re-establish populations of the endangered red wolf, which became extinct in the wild about 1975 (Wayne 1996), were controversial because of the possibility of past hybridization. Previously, some scientists had argued that such hybridization had already occurred. They asserted that the red wolf was not a true species, citing genetic studies that found no definitive genetic features in

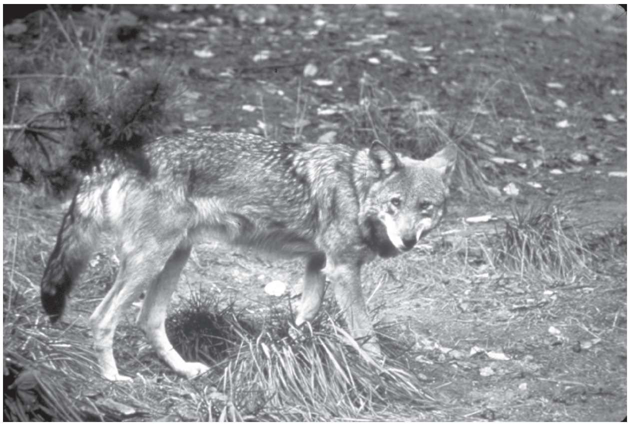


FIGURE 6.20. The red wolf (*Canis rufus*), a species threatened with genetic extinction through hybridization with and introgression from gray wolves (*Canis lupus*), coyotes (*Canis latrans*), and dogs (*Canis familiaris*). (Photo courtesy of R. B. Forbes and the Mammal Images Library of the American Society of Mammalogists.)

the red wolf or any definitive pattern of genetic phylogeny that could distinguish red wolves from coyotes (Wayne and Jenks 1991; Roy et al. 1994a, b). Such data led some to argue that the captive breeding program and proposed reintroduction of the red wolf should be abandoned (Ezzell 1991), despite the fact that red wolves are physically distinct from other canids. Morphological examination of museum specimens supports the view that the red wolf is distinct from the coyote (*Canis latrans*). Further, early twentieth-century specimens of the gray wolf from central Texas are distinct from red wolf-coyote hybrids that were known and collected from that area at the same time (Novak 1999). Fossil remains of wolves from Florida have cranial measurements identical to red wolves, not gray wolves, leading to the theory that the red wolf represents a surviving line of "small primitive wolves that once occurred throughout the Holarctic and that formed an evolutionary stage between the coyote and the modern gray wolf" (Novak 1999:145). Whether similarities of DNA with other canids represent recent introgression or the acquisition of DNA from other species through hybridization in the more distant past, the case of the red wolf reveals the dangers of genetic introgression for a species at low numbers when confronted by sympatric, closely related, and reproductively compatible species that exist around it at high numbers.

The US Fish and Wildlife Service persisted with its captive breeding program and reintroduction plan despite criticisms, eventually releasing red wolves at the Alligator River National Wildlife Refuge in northeastern North Carolina and Great Smoky Mountains National Park in eastern Tennessee. These efforts have shown promising initial success, but could yet be hindered by hybridization between red wolves and coyotes or domestic dogs (*Canis familiaris*) because there were still only about 100–200 red wolves in the wild population in 2007, and probably less than 100 animals in any single population. Currently hybridization and introgression are considered the greatest threats to the persistence of the red wolf. In this case, the greatest danger is not from "simple hybrids" produced by pairings between red wolves and coyotes, but from back crossing between red wolves and red wolf-coyote hybrids, a path of introgression that could eventually eliminate all remaining "pure" red wolves. Fredrickson and Hedrick (2006) estimated the risk posed by these threats by constructing an individual-based simulation model to predict the future trajectory of red wolf populations. In model outcomes, the number of red wolf pairs increased quickly to carrying capacity when coyotes were not present. When coyotes were present and pairing among red wolves and red wolf-coyote hybrids was random, 80% of simulated red wolf populations were exterminated within 50 years (Fredrickson and Hedrick 2006).

The most effective management technique to protect a species vulnerable to hybridization and introgression is to sterilize paired individuals of the more common species in the immediate area, in this case paired coyotes and paired hybrids. But this can be difficult when appearance is the only criterion one can use in the field. Nevertheless, a sterilization strategy is feasible, and Fredrickson and Hedrick modeled outcomes of three strategies: no sterilization, low sterilization (50% of hybrid and coyote pairs are sterilized when proportion of mixed pairs in the red wolf population exceeds 0.40) and high sterilization (75% of hybrid and coyote pairs sterilized when proportion of mixed pairs exceeds 0.10). They combined these three management strategies with three mating scenarios: random mating (red wolves, coyotes, and hybrids select mates without discrimination in these categories), weak assortative mating (red wolves do not mate with coyotes, but randomly choose between other red wolves and hybrids), and weak assortative mating plus "red wolf challenges." The last phrase refers to the fact that single red wolves and red wolf pairs have been observed to challenge and displace hybrid pairs and single hybrids from their territories, thus reducing the proportion of hybrids in the breeding population. Fredrickson and Hedrick developed algorithms to predict the occurrence and outcomes of such challenges, and fed the results back into the model so that challenges had an ongoing effect on population composition. With these parameters in place, note the dramatic effect of a high sterilization effort on red wolf persistence, especially where red wolf challenges are assumed, as displayed in Figure 6.21. Where a high sterilization effort is used as a management strategy and red wolf challenges occur at predicted rates, the red wolf population rises quickly to carrying capacity (50 pairs) and persists at that level for the length of the simulation (50 years). In this scenario, only 0.3% of colonizing populations were predicted to become extinct after 50 years. At the other extreme of no sterilization and random mating, the population declines to a low and highly vulnerable number of animals (ten pairs) after 50 years. In this case, the model predicted extinction of 79.9% of colonizing populations (Fredrickson and Hedrick 2006).

6.7.2. Importing Genetic Diversity: Genetic Restoration of Inbred Populations

We see in the case history of the red wolf the potential and highly dynamic interaction between mating patterns and management strategies that can affect the fate of a species vulnerable to hybridization and introgression, but the complexities of hybridization and introgression are not confined to the Canidae. The Florida panther also faces issues of genetic integrity that have both legal and biological ramifications. The Florida panther is an endangered subspecies of mountain lion (also known as cougar, catamount, or puma) that once ranged throughout the southeastern United States but is today confined to the Everglades and Big Cypress Swamp of southern Florida. In the late 1980s researchers discovered

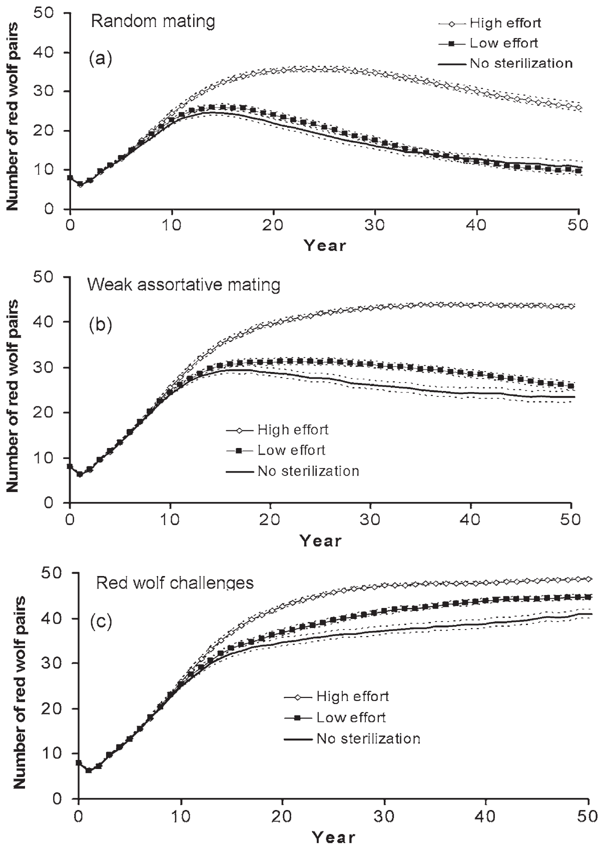


Figure 6.21. Mean numbers of red wolf pairs in nonextirpated wolf populations over time when there is high or low sterilization effort of coyote and hybrid pairs with (a) random mating among red wolves, coyotes, and hybrids, (b) weak assortative mating, and (c) red wolf challenges that displace hybrid pairs. Broken lines represent 95% confidence intervals. (Fredrickson and Hedrick 2006. Dynamics of hybridization and introgression in red wolves and coyotes. *Conservation Biology*. Copyright 2006 by Blackwell Publishing.)

two distinct genetic strains in the remaining individuals of the Florida panther population. One strain was associated with the main population in the Big Cypress Swamp, the other was identified in two family groups that had appeared in the Everglades. Genetic analysis demonstrated that the Everglades individuals were distinct not only from the Big Cypress panthers, but also from western US mountain lions. Their genetic characteristics were closer to subspecies from South and Central America (O'Brien et al. 1996). Inspection of the archives of the Everglades National Park revealed that between 1957 and 1967, seven animals from a captive stock had been released into the Everglades with National Park Service cooperation. This stock was derived from a mixture of Florida panthers and individuals from South American subspecies (O'Brien et al. 1990). Unfortunately, as noted earlier, the US Endangered Species Act does not protect hybrids between endangered taxa because such hybrids are not considered to protect or help the recovery of listed species, and hybrids could jeopardize the continued existence and genetic integrity of the protected taxa. This legal understanding of the ESA, established through actual court cases, has become known as the "hybrid policy," and meant that Florida panther was no longer subject to legal protection under the US ESA. However, the hybrid policy was subsequently suspended in order not to penalize species because of "a bureaucratic precedent that did not anticipate the resolving power of molecular genetics" (O'Brien et al. 1996). Instead, the Florida panther became the beneficiary of a "genetic restoration" program in which females from a Texas population of mountain lions, the closest natural population, were introduced into the Florida population (Hedrick 1995), and offspring of these females show reductions in inbred traits (Land et al. 1999).

Hybridization itself may not always be a threat to conservation, but could, in some cases, be an asset to it. In cases like the Florida panther, genetic restoration of a highly inbred population may be accomplished by introducing individuals from closely related populations, producing hybrids with greater genetic diversity and higher fitness. For example, an isolated population of an adder (*Vipera berus*) in southern Sweden was the subject of such a genetic rescue in which 20 males of the same species from another population were captured and released into its site over a 3-year period. Both total numbers and recruitment increased over the next 3 years after the release (Madsen et al. 1999). A similar genetic restoration effort was conducted on a remnant population of greater prairie chickens (*Tympanuchus cupido pinnatus*) in Illinois, and with similar signs of recovery (Hedrick and Kalinowski 2000).

These kinds of introductions should not be attempted carelessly. All three of the previous examples were cases in which the threatened population was in serious danger of further decline, and new animals selected for introduction were chosen with careful scientific study. Without these and other kinds of appropriate safeguards and selection, the introduction of new animals into an inbred and declining population could have detrimental rather than positive effects. If the new animals have been bred in captivity, they will lack appropriate adaptations to natural environments. If new individuals are from wild populations adapted to an entirely different array of natural conditions and environmental tolerances, the introduction could be a disaster. "Genetic rescues" like those performed for the Florida panther, the adder, and the greater prairie chicken should not be attempted except in cases of dire need and extremely well informed scientific understanding of the potential effects of the introduction.

Compared to animals, plants hybridize much more freely, and their resulting hybrids can have conservation value in both natural systems and in planned conservation management. To better appreciate the value of such hybrids in plants, we now examine some specific cases unique to plants in which that value is expressed.

6.7.3. Hybridization in Plants – Conservation Threat or Conservation Asset?

Unlike animals, where hybridization is relatively rare and hybrids are often infertile, plants hybridize freely and hybrid offspring may be capable of mating with one another and with either parental species. Thus, plant ecologists have long considered hybridization a normal phenomenon in plant populations and an important contributor to adaptation and subsequent speciation (Stebbins 1950; Grant 1971; Lewis 1980).

Plant conservationists working in the field suspect that the hybridization of rare species with closely related, common species is threatening a large number of rare plants with extinction. For example, land stewards of The Nature Conservancy in the United States cited a number of rare or endemic species in the western US that are believed to be in danger of extinction through hybridization with other species. These include endangered, threatened, or candidate endangered species such as white firewheel (*Gaillardia aestivalis*), Bakersfield saltbush (*Atriplex tularensis*), western bog lily (*Lilium occidentale*), Nelson's sidalcea (*Sidalcea nelsonii*), and peacock larkspur (*Delphinium pavonaceum*). However, the accounts of hybridization in these species exist largely in the form of unpublished government or agency reports, and none is supported by molecular experiments or evidence (Rhymer and Simberloff 1996). This lack of publication or molecular data does not mean that these concerns are unwarranted. It does, however, reveal, that potential threats from hybridization in plants can occur rapidly, and can potentially produce extinction before conservationists are able to enjoy the luxury of careful scientific experimentation and study.

Although hybridization can be a threat to plants, just as in animals, there is growing field and experimental data that zones of active plant hybridization also are zones of high levels of biodiversity in non-plant taxa, especially insects and fungi (Whitham et al. 1999). For example, in zones of hybridization among different species of *Eucalyptus* in Australia, 29 of 40 insect and fungal taxa examined were more abundant in hybrid zones than in "pure" zones (Whitham et al. 1999). This occurred primarily because hybrid trees accumulated insect and fungal species that were otherwise unique to each parent species, thus producing the genetic equivalent of an "edge effect" (Figure 6.22). More controlled experiments in specially created "hybrid gardens" supported these field observations. Thus, hybridization in plants may be an asset to conservation rather than a liability because it is positively correlated with, and may provide an underlying genetic basis for, higher levels of community biodiversity. After reviewing both field and experimental evidence, Whitham et al. (1999) concluded that, in plants, "hybrid zones can be centers of biodiversity."

The Australian pattern is repeated in North America, especially in ecologically important and conservation sensitive riparian zones. In the western United States and Canada, the dominant trees of riparian zones, especially at lower elevations, are cottonwoods (*Populus* spp.) of various

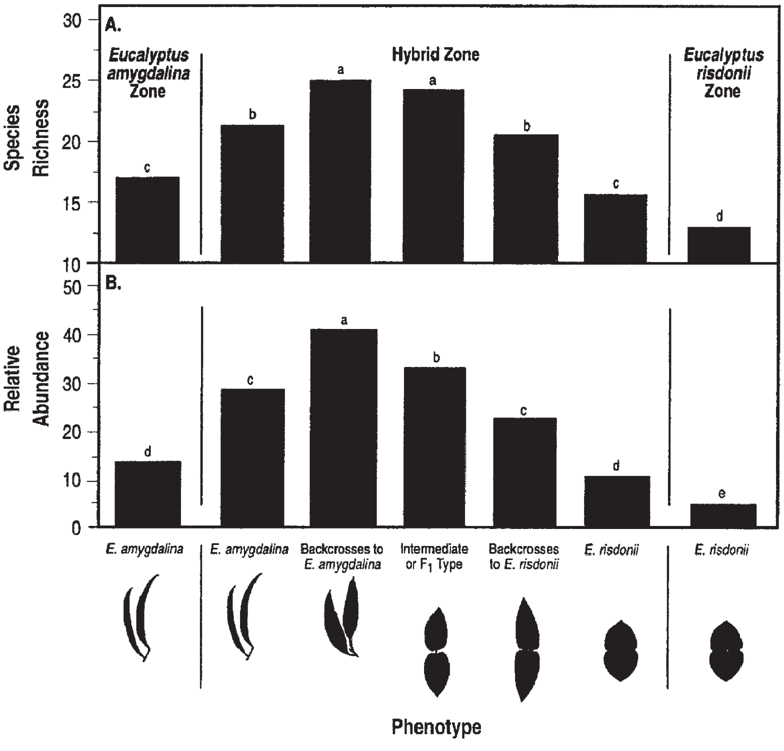


FIGURE 6.22. Species richness and relative abundance of 40 insect and fungal taxa increase on hybrid *Eucalyptus* compared to parental trees in pure stands or intermixed with hybrids. Groups with different letters are significantly different from one another. (Whitham et al. 1999. Plant hybrid zones affect biodiversity: tools for a genetic-based understanding of community structure. *Ecology* 80:416–428. Reprinted by permission of the Ecological Society of America.)

species which naturally and readily hybridize in areas where different species overlap in range. Hybridization is very common between the broadleaf cottonwoods, especially Fremont cottonwood (*P. fremontii*) and plains cottonwood (*P. deltoides*), and the narrowleaf cottonwood (*P. angustifolia*), which hybridizes with Fremont cottonwood on the west (Pacific) slope of the North American and with plains cottonwood on the east (Atlantic) slope of the Continental Divide. Randy Bangert and his colleagues tested the hypothesis that cottonwood hybrid zones formed in these species would exhibit higher levels of arthropod diversity than non-hybrid zones. This belief rests on the fact that many species of arthropods, especially leaf-modifying insects, are highly specific to particular plant species and even to particular leaf forms. In a cottonwood hybrid zone, as the variety of leaf forms increases due to hybridization, the variety of arthropods also should increase.

Bangert and his colleagues addressed the question at multiple landscape scales within and throughout the western US states of Arizona, Colorado, New Mexico, and Utah on both sides of the continental divide, thus examining riparian habitat in river systems flowing to both the Atlantic and Pacific Oceans. They first measured the alpha-diversity of arthropods within cottonwood cross-types in riparian zones in individual drainages, and then the beta-diversity of the arthropod community among different cottonwood cross types in different drainages, building in analyses of the effects of differences in river, slope and drainage. Results were consistent with predictions. In individual riparian zones (specific sites), the highest levels of arthropod species richness (alpha diversity) were associated with the most genetically diverse cross types of cottonwoods (Figure 6.23a). Within a given river system, hybrid zones averaged 1.49 times greater species richness that pure broadleaf zones. Hybrid zones also had the greatest levels of host-plant genetic diversity and supported significantly different arthropod communities than parental types. The differences were greatest between hybrids and broadleaf cottonwoods, with leaf-modifying arthropod diversity being 1.46–1.54 times higher in hybrid zones than in broadleaf zones. Backcross trees (hybrids crossed back to a parental type) had more arthropod species than broadleaf trees and, overall, habitats with the highest levels of hybrid diversity had the highest levels of arthropod diversity. Hybrid zones had the highest levels of species richness, and had more arthropod species than broadleaf zones, although not more than narrowleaf zones. In their examination of beta diversity across multiple river systems, Bangert and his colleagues found that there were river and slope effects on arthropod communities, and high between-community diversity among arthropod communities found in different cross types. However, there was no interaction of effects between slope (Atlantic versus Pacific) and cross-type, indicating that the effect of cross-types on arthropod diversity was a

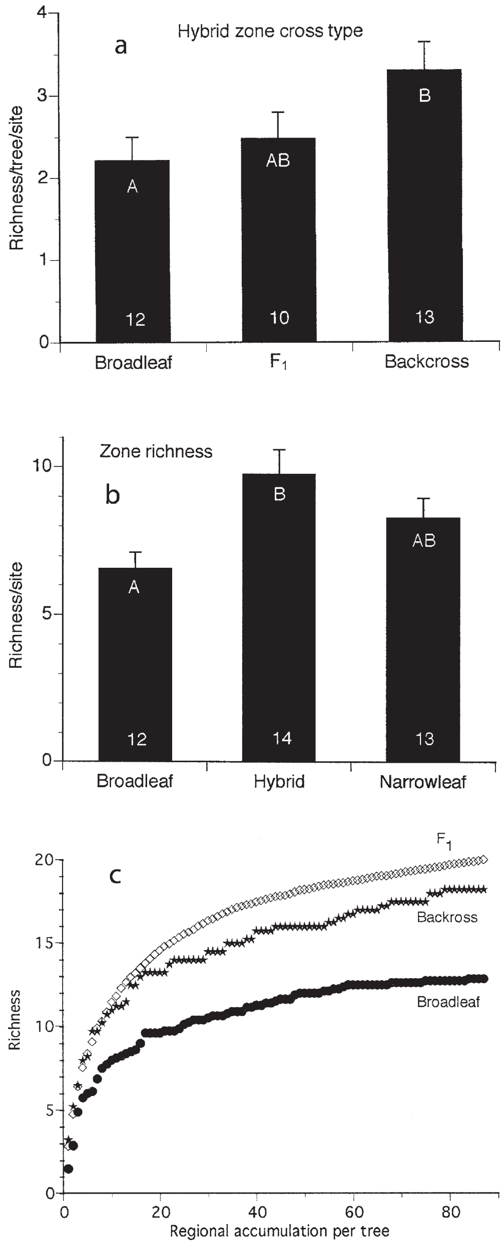


FIGURE 6.23. (a) Mean arthropod richness by cottonwood cross type per hybrid zone ± one standard error (bars), a measure of arthropod alpha (site specific) diversity in different kinds of trees and (b) mean arthropod richness in three hybrid zones across replicate rivers, a measure of arthropod beta diversity in different cottonwood cross type associations across a landscape. Note the higher levels of species richness associated with hybrid zones at both scales. (c) Accumulation of species richness per tree for all cottonwood cross type zones across the extent of all river systems in the study area (Arizona, Colorado, New Mexico, and Utah, USA). Note that, although broadleaf (parental) cottonwood types add few additional species after approximately 50–60 trees, hybrid zones continue to add species beyond 80 trees. Different letters represent statistically significant differences between cross types. Numbers at bases of bars indicate the number of replicate hybrid zone sites (a) or rivers (b). (Bangert et al. 2005. Benefits of conservation of plant genetic diversity to arthropod diversity, *Conservation Biology*. Copyright 2005 Blackwell Publishing.)

stable and consistent effect on both sides of the Continental Divide. The pattern of increased arthropod diversity in cottonwood hybrid zones was consistent at both local and regional scales. Over the same distance, hybrids zones had greater zone richness than broadleaf zones (Figure 6.23b) and species richness accumulated faster in hybrid zones than in broadleaf zones (Figure 6.23c).

Reflecting on the results of this study, Bangert et al. note that "… several of these leaf-modifiers [arthropods] increase the diversity of free-living arthropod and avian communities … so even small differences in leaf modifier richness could result in large differences in overall diversity" (Bangert et al. 2005:387). Seeing that all cottonwood hybrid cross types appear necessary to maintain maximum host-plant diversity, Bangert et al. concluded that "… we need to rethink the reputed negative role of hybrids in ecology and conservation.… Where there is high genetic variability among plants, herbivore density should be greatest … Therefore natural hybrid zones may represent diversity hotspots and should be focal points for the conservation of biodiversity and ecological and evolutionary processes" (Bangert et al. 2005:387–388).

As studies on hybrids have revealed their importance to community biodiversity, the original prohibition of the US Endangered Species Act against listing hybrids has been removed. Hybrid species are now considered on a case-by-case basis, and two species of hybrid plants are now listed and protected under the US ESA.

These examinations of eucalyptus and cottonwood systems are studies of the effects of common species on biodiversity conservation, but hybridization also can be of value in the preservation of endangered species and their genetic diversity. The Catalina Island Mahogany (*Cercocarpus traskiae*) grows only in one ravine on the south-west side of Catalina Island off the California coast. Even when initially discovered in 1897, the population consisted of only 40 individuals. Today that number has been reduced to six. But the Catalina Island Mahogany will hybridize with its more abundant relative, *Cercocarpus betuloides*. Identifiable hybrids on the island, many of which are still in the seedling stages, are estimated to contain 50% of the Catalina Island's Mahogany's genetic diversity. Their loss would significantly reduce the diversity of this population even if the genetically pure individuals were preserved. An even more obvious example of the value of hybrids in plant conservation can be seen in the case of the American chestnut, *Castanea dentata*. Decimated in North America by a disease, the chestnut blight, there are now active efforts to transfer disease-resistant genes from the Chinese chestnut, *Castanea mollissima*, into the American chestnut through carefully planned back-crossings. In this effort. hybrids produced from matings of *C. dentata* and *C. mollissima* are then crossed back to *C. dentata*. Individuals that show resistance to the chestnut blight are selected for continued breeding with pure *C. dentata*. Through such planned and controlled introgression, conservation geneticists hope to one day produce a tree that is morphologically and genetically an American chestnut, but can resist the chestnut blight and return to its place in the North American forest (Carney et al. 2000).

6.7.4. Introgression from Genetically Modified Organisms

Genetically modified organisms (GMOs), or, as they are called in some parts of the world, ***living modified organisms*** (LMOs) constitute a special category of genetic "hybridization" that presents serious potential concerns to conservation biology. Developed to improve the performance and productivity of economically important varieties of plants and animals, LMOs are organisms whose genomes have been engineered or "spliced" so as to incorporate genes from other, usually very different, kinds of organisms in order to preserve, enhance, or add traits favorable to increased production, fertility, survivorship, or adaptability to particular environmental conditions. To take one fairly benign example, *Escherichia coli*, a bacterium that lives in the lower intestine of many birds and mammals, and is commonly used in biological experiments and education, can be made to incorporate a gene for bioluminescence from the genome of the jellyfish, *Aequorea victoria*, so that colonies of the transformed *E. coli* will glow with a bright green color in the dark if illuminated with an ultraviolet light.

Perhaps few persons would object to the prospect of bacteriologists being able to see their specimens better in a dark room, but what if genetically transformed organisms should, somehow, return to the wild and breed with non-transformed populations? What kind of offspring would result, and could there be negative effects? Questions like these led the Members of the Conference to the Parties to the Convention on Biological Diversity (CBD, Chapter 3) to recognize the special significance of LMOs. In their development and implementation of the CBD, the delegates agreed to develop a protocol on LMOs for the sake of safety and for the conservation of biodiversity. This effort began with negotiations starting in the mid-1990s which continued for several years, finally culminating in special meetings of the delegates, first in Cartagena, Columbia, and then in Montreal, Canada, where an agreement called the BioSafety Protocol was signed in January 2000. The Protocol went into effect in September 2003, and now has more than 130 contracting parties. The Protocol offers recommendations for the safe transfer, handling, and use of LMOs in such ways that they will not pose a threat to humans or to other species. It provides for an Advance Informed Agreement (AIA) procedure which permits parties considering transfer of LMOs to decide, in advance and informed by scientific risk assessment, whether or not to accept imports of LMOs.

The Protocol also provides for a risk assessment framework, an information clearinghouse, and a procedure for documenting international shipments of LMOs. Finally, the Protocol requires contracting parties to develop, in advance, rules and procedures regarding potential liability and redress regarding any harm or damage that might result from international shipments of LMOs (Hill and Sendashonga 2006).

So far, there are no known cases of LMOs causing a decline or extinction in any extant population. One experimental study did show that high doses of the Bt gene, which is present in genetically modified corn and some other food crops, caused mortality in larvae (caterpillars) of monarch butterflies (*Danaus plexippus*) (Losey et al. 1999), but the dosage ingested by the caterpillars was so much higher than actual levels of Bt in field crops that the risk was judged to be insignificant (Sears et al. 2001). As with Bt, most LMOs are crop plants, but there are LMOs, already produced or under development, that include transgenic fish, viruses, and insects. With the exception of one aquarium fish, these nonplant LMOs are not yet widely available, but proposals for producing transgenic fish, including tilapia (*Oreochromis* spp., *Sarotherodon* spp., and *Tilapia* spp.) and Atlantic salmon (*Salmo salar*), in aquacultures are being considered in Canada, Cuba, and the US (Hill and Sendashonga 2006). The potential impacts of an escape of transgenic fish of these or other species (tilapia is now a worldwide food commodity, and the sixth most popular seafood in the US) are profound. As environmental policy analysts Ryan Hill and Cyrie Sendashonga note, “If such fish were to escape from aquaculture facilities, potential ecological risks include indirect competition with wild fish and decreased fitness of wild populations through hybridization …” (Hill and Sendashonga 2006:1622).

It would certainly be premature, as well as ignorant, to say overmuch about a threat to genetic biodiversity that is still only potential and hypothetical. Nevertheless, unauthorized use or release of LMOs could cause serious genetic deterioration in wild populations. Many of the details of the Cartagena Protocol are still being formalized. While the Protocol is being defined, conservation biologists may have a window of opportunity to influence delegates, policy makers, and other government officials in developing and enforcing the Protocol in such a way as to maximize the protection of biodiversity and minimize the genetic risks of LMOs to it.

6.8. Outbreeding Depression

Although usually less significant in its effects, or perhaps simply less studied, than inbreeding depression, the problem of ***outbreeding depression*** deserves mention, both to define the concept and to note the characteristics of populations that may suffer from its effects. As the external environment may mold local adaptations by natural selection, the internal genetic environment of a population may lead to the production of local complexes of genes that interact in a mutually favorable manner. Thus, population subunits that are highly adapted to local conditions (a condition common in metapopulations) and that have low vagility may evolve coadapted gene complexes, in which genes must be inherited together to produce appropriate adaptive effects. When individuals from such normally inbreeding populations breed with individuals from other populations of the same species (“outbreed”), they may decline in fitness as their uniquely coadapted genetic combinations are disrupted. Outbreeding depression is most common in plants (Frankham 1995a), especially in populations that have evolved high levels of self-pollination (“selfing”). In fact, selfing has evolved repeatedly in plant taxa that were previously outcrossing (Stebbins 1957; Grant and Grant 1965; Raven 1979). Selfing is particularly adaptive where pollinators are at low density and the accompanying probability of being pollinated is low. In the annual and perennial herb genus *Epilobium*, for example, selfing and outcrossing populations are sympatric, often growing on the same site. For example, *Epilobium ciliatum* is mostly self-pollinating, while the closely related species *E. angustifolium* is usually outcrossing. In forest clearcuts of the US Pacific Northwest, both species often invade the same site after trees are removed. Parker et al. (1995) compared the relative levels of inbreeding depression in these sympatric species and found, not surprisingly, that inbreeding depression was significantly lower in the outcrossing *E. angustifolium* than in selfing *E. ciliatum*. Poor reproductive performance (outbreeding depression) also was documented in individuals of *E. ciliatum* that did not self-pollinate (Parker et al. 1995).

Although far less common than in plants, outbreeding depression is also a potential genetic problem in animals. One of the most fascinating examples is found in the collared lizard (*Crotaphytus collaris*) (Figure 6.24) of the Ozark Mountains of the south-central United States (Templeton 1986). Today the collared lizard lives primarily in dry grasslands and deserts in the southwestern US, but its range previously extended further east. When, in recent centuries, the eastern portion of its range became wetter and more forested, the collared lizard declined in these regions. Declines were exacerbated by fire suppression that reduced or eliminated tallgrass prairies in the southeast where the lizard still survived. Today the only eastern remnants of the species are populations in the Ozark Mountains, mainly in Arkansas. There lizards survive in small openings (glades) associated with rocky soils and outcrops, but will not disperse through the surrounding oak-hickory forests to other glades. As a result of an estimated 2000 generations of isolation among populations averaging fewer than 50 individuals, intra-glade populations have become genetically identical. A small number

FIGURE 6.24. The collared lizard (*Crotaphytus collaris*), a species whose local, highly inbred populations could be negatively affected by outbreeding. (Photo courtesy of US Fish and Wildlife Service.)

of genes also appear to exist together in a co-adapted gene complex, with the genetic structure of the complex slightly different in each glade (Templeton 1986).

Although outbreeding depression has not been explicitly documented in the collared lizard, this species illustrates two forces that can allow outbreeding depression to occur. One is the phenomenon of *local adaptation* and accompanying genetic differentiation. The second is ***intrinsic coadaptation***, in which genes in a local population primarily adapt to the genetic environment defined by other genes. This latter phenomenon can occur in a species that becomes subdivided into small, isolated populations. Outbreeding depression associated with intrinsic coadaptation is normally a temporary phenomenon eliminated by natural selection, but it has become a more permanent fixture of these glade-specific populations of collared lizards.

The collared lizard presents unique genetic considerations for conservation efforts that attempt to establish new populations in currently unoccupied glades. In new glades, individuals from different populations must be used in the founding group. Initially the problem of outbreeding depression was a serious consideration in these conservation efforts. However, after careful review, outbreeding depression is no longer expected to have any deleterious effects on founding populations. The co-adapted gene complex is expected to either be preserved in the founding population (because the number of genes in the complex is small) or selection is expected to quickly and efficiently establish a new parental genotype of high fitness (Templeton 1986).

6.9. Synthesis

Through a unique combination of technological empowerment, legal incentive, and conservation initiative the field of conservation genetics has become one of the most important dimensions of conservation biology today. Increasing precision and quantification of the genetic characteristics of individuals and populations, the techniques of which we will discuss in the following chapter, has given added force, along with occasional dilemmas and confusion, to landmark legislation like the Convention on the International Trade in Endangered Species (CITES), the US Endangered Species Act and its subsequently developed counterparts in countries throughout the world, and many other conservation laws that require taxonomic clarity to be applicable to the protection of species. And in cases where taxonomic distinctness is an important criterion for setting conservation priorities, genetic analyses take pride of place in decisively answering questions of taxonomic status (Schemske et al. 1994).

The attention to conservation genetics is not undeserved. Although it is the individuals of living species that are visible and present to us, without the conservation of their invisible genetic diversity to adapt to a living and changing environment, the species would soon pass from our eyes and remain only a memory in the mind. An understanding of the theoretical basis for genetic conservation, although it forces us to consider genetic units and mathematical–conceptual relationships that at first seem only intellectual abstractions, begins to reveal to us exactly what genetic diversity *is*, why inbreeding can lead to a population's decline, and why processes of gene flow matter to our conservation efforts, not only for populations *per se*, but with regard to questions of habitat fragmentation, dispersive ability, and population structure.

Although it was neither possible nor advisable to exclude every concrete example and application from a chapter devoted primarily to the *theory* of conservation genetics, the applications of such theory deserve their own elaboration in their own place, and they will have both in the next chapter. As you study the chapter that follows, move regularly and frequently back to the theoretical foundations laid here. When theory and application are understood as an integrated whole, sound judgment and insight begin to be a regular part of management decisions intended to conserve genetic biodiversity.

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7

Genetic Management – Managing Genetic Diversity for Conservation Goals

> *If conservation genetics is to develop from a phenomenological crisis discipline, which concentrates on case studies, into a multidisciplinary science searching for the general principles that are involved in determining extinction probabilities of … populations, it is also necessary to study common species within the context of the conservation genetics paradigm.*
>
> N. J. Ouborg, P. Vergeer, and C. Mix 2006

In this chapter you will learn about:

1. **Techniques for making genetic assessments of individuals and populations and how to interpret their findings**
2. **Strategies for maintaining genetic diversity in captive populations**
3. **Applications of genetic techniques and assessment in the conservation of wild populations**
4. **Building genetic considerations into conservation plans for population management and design of nature preserves**

7.1. Conservation Genetics: From Theory to Application

In the previous chapter, we examined the historical development and theoretical basis for the growing field of conservation genetics and its potential role in the conservation of biodiversity. Understanding such historical, conceptual, and mathematical underpinnings of genetic structures is vital to understanding what genetic analyses can do to solve conservation problems, and how the data associated with such solutions should be interpreted and understood. But conservation in the modern world can never afford to remain exclusively theoretical for long. Ouborg et al. (2006) warn us above that conservation biology cannot mature as a science without learning to apply its theories to both common and endangered species. In this chapter, we examine the specific techniques that have been developed to more precisely assess the genetic status of populations, endangered and otherwise, and the use of the data they provide to solve the problems of maintaining genetic diversity in captivity and in the wild. We begin with an examination of the procedures and techniques that have given genetic analysis its current technological power in conservation studies.

7.2. Genetic Techniques: Solving the Problem of Assessing Genetic Status and Change

7.2.1. General Considerations

It is not merely increased concern over genetic variation that has driven the science of genetics to prominence in conservation biology, but also increasing precision and sophistication of techniques associated with genetic analysis, particularly at the molecular level. It is beyond the scope of this chapter to review all of the genetic techniques currently used to assess genetic variation in individuals and populations, but we will examine the principles, procedures, strengths, and weaknesses of the techniques that are used most widely in conservation and that appear most often in current conservation biology literature. Appreciating what individual techniques can and cannot do can help not only to choose the right technique to solve the right problem, it is also essential for interpreting and assessing the validity of genetic studies and preventing misinterpretations and inappropriate applications of results gained from them.

7.2.2. Allozyme Electrophoresis: Genetic Variation at Molecular Levels

Geneticist R. C. Lewontin, recalling the changes he observed in genetics during his career, said, “When I entered Th. Dobzhansky’s laboratory as a graduate student in 1951, the problematic of population genetics was the description and explanation of genetic variation within and between populations. That remains its problematic 40 years later in 1991. What has changed is our ability to characterize variation at the genic and nucleotide level and, linked to the ability to give detailed descriptions of variation, the development of a theory of population genetics that takes into account the full implication of historical ancestries in real populations” (Lewontin 1991).

The technique that began the revolutionary transition from Mendelian genetics to molecular genetics was ***gel electrophoresis*** of proteins. It had long been known that a point mutation in the coding sequence of a molecule of DNA would result in an amino acid substitution in the protein synthesized from that sequence. Theoretically, that substitution should be detectable by analyzing the protein. The protein could then be compared with non-mutated proteins from other individuals and used as an index of genetic variation among them. But the laboratory methods of protein analysis were so time consuming and laborious as to be impractical for genetic surveys.

Protein electrophoresis made such analysis feasible. It was already known that a single amino acid substitution in a protein could change the physical configuration and charge of a protein enough to cause it to move at detectably different rates in a charged field. This movement could be observed visually in a gel by treating proteins with different types of stains. Differences in movement rates could be used to infer differences in amino acid sequences, and such differences could be treated as a legitimate index of genetic variation in different individuals. When such methods were adapted to large-scale surveys of individual genomes from natural populations, science had a powerful tool in hand for practical assessment of genetic variation at molecular levels (Lewontin 1991).

Allozymes refer to different allelic variants found at a single gene locus. Allozymes bear electrical charges, which differ among allozymes as a reflection of differences in their enzyme proteins. In ***allozyme electrophoresis***, allozymes with different charges are separated through movement in a chemical medium (gel) to oppositely charged poles in an electric field (Leberg 1996), thus moving through the gel at different rates. The common way to visualize an allozyme in a gel exploits the charged, enzymatic nature of the allozyme. The gel is incubated in a colorless mixture of reactants that can be modified by the allozyme. The modification produces a colored product that stains the gel, producing discrete bands of color, which also are usually of different lengths that reflect different rates of allozyme movement (Figure 7.1).

Because allozyme composition, and corresponding charge characteristics, are controlled by the sequence of nucleotides in DNA, charge differences are assumed to represent differences in DNA sequences (Leberg 1996). Thus, allele frequencies determined by allozyme analysis are based on the assumption that different allozymes are unique in their staining patterns because of differences in their nucleotide sequences. Genetic analyses of populations can determine the frequency of these alleles. Through these analyses, relationships between populations inferred from allozyme data are based on the similarity of allele *frequencies,* not on the similarity of the alleles themselves. Allozymes are of interest to conservation biologists because their polymorphisms permit comparisons among different individuals, populations, or species that can be useful in showing degrees of relatedness. They can be obtained from almost any type of tissue, although tissues rich in protein are generally used.

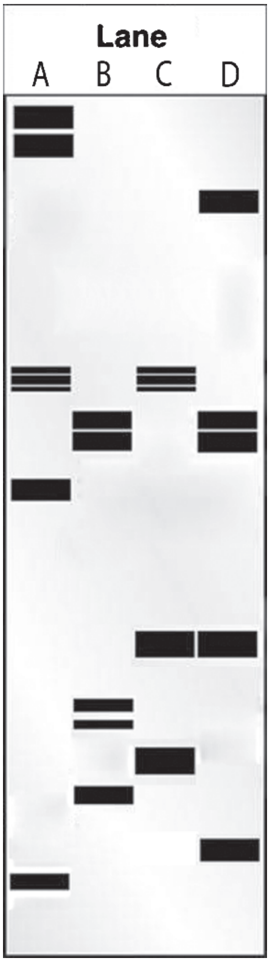


FIGURE 7.1. An example of four DNA “fingerprints” from different individuals generated by gel electrophoresis. Each lane (column) represents one individual. (Illustration by M. J. Bigelow.)

Leberg (1996), in a comprehensive review of allozyme electrophoresis, noted nine different potential and actual applications of this method in conservation genetics. These are estimation of genetic variation, determination of association of genetic diversity with fitness and population viability, determination of effective population size, rates of gene flow, types of mating systems (degree of inbreeding avoidance) used in the population, population structure, degree of hybridization, identification of paternity and species determination, and resolution of phylogenetic relationships. Most of these applications could also be addressed by other genetic techniques, which will be treated in detail later.

By itself, the development of gel electrophoresis need not have produced any important implications for conservation. Prior to the development of allozyme electrophoresis, geneticists debated about the role of variation in natural populations and the average levels of variation that should be expected in them. The so-called “balance” school asserted that individuals in sexually reproducing populations were heterozygous at most loci, whereas the “classical” school believed that most loci were homozygous (Lewontin 1991). Experiments in Mendelian genetics had failed to resolve the argument, but experiments in electrophoresis confirmed high levels of variation and heterozygosity in most populations. This outcome had two important implications: (1) precise detection of genetic variation among individuals and populations, and (2) empirical evidence that such variation was common in most populations. Data gained from electrophoresis supported the idea that most populations maintained high levels of genetic variability, possibly as a means of coping with recurrent environmental variation. Electrophoresis also played an important role in determining the genetic and taxonomic identities of endangered species and their relationships to more abundant, closely related species.

Allozyme electrophoresis was one of the first molecular techniques to offer a sensitive assay of genetic variation, and is still one of the most widely used. Through the early 1990s, more genetics papers published in the journal *Conservation Biology* used allozyme electrophoresis than all other methods combined (Leberg 1996). Electrophoresis no longer holds primacy in conservation as other molecular techniques have become more available and precise, but it continues to play an important role, especially when used with other tools of genetic assessment. For example, electrophoresis has more recently been used in combination with other techniques to separate genetic markers as a means of visualizing and identifying ecologically important genetic traits in populations (van Tienderen et al. 2002) and in scoring genetic profiles to compute the value of population adaptive indices (PAI), a genetic diversity index that provides a quantitative measure of the adaptive value of the overall genetic diversity of the measured population (Bonin et al. 2007).

7.2.3. The Polymerase Chain Reaction: A Non-invasive Method for Genotyping Endangered Species

The development of the ***polymerase chain reaction*** (PCR) as a standard genetic technique revolutionized conservation biology beginning in the late 1980s. This non-invasive technique for determining genotypes of individual animals is based on a relatively simple reaction, in which a short region of a DNA molecule, even as small as a single gene or smaller, is copied repeatedly by a DNA polymerase enzyme. In standard PCR, any region of a DNA molecule can be chosen as long as the borders (beginning and ending sequences) are known. To carry out the PCR, two ***oligonucleotides*** (short pieces of DNA) hybridize to the DNA molecule, one to each strand of the double helix. These act as primers for the subsequent DNA synthesis and delimit the region to be amplified. An enzyme, DNA polymerase I, is added from the bacterium *Thermus aquaticus*, an organism native to hot springs whose enzymes, including its DNA polymerase (known as *Taq)*, resist denaturization when exposed to heat (Brown 1995). The *Taq* enzyme is incubated in the solution and facilitates the production of new complementary DNA strands. The mixture is then heated so that the new strands detach from the original DNA, then the strands are cooled, allowing more primers to hybridize at their respective positions, including positions on the newly synthesized strands (Brown 1995). The *Taq* enzyme carries out a second round of DNA synthesis and the cycle can be repeated many times, eventually resulting in the synthesis of several hundred million copies of the amplified DNA fragment which can then be analyzed in various ways (Brown 1995). The most common and useful analysis in conservation is direct sequence analysis of the PCR products, resulting in an identification of the genotype of the organism from which the material was obtained. The products also can be seen visually by electrophoresis in an agarose gel after staining with dyes (Fritsch and Rieseberg 1996) (Figure 7.2).

PCR analysis can be used as postmortem technique, such as on museum specimens (Morin and Woodruff 1996), and only minute amounts of DNA are required. The analysis can include genetic fingerprinting to identify particular individuals. Using Reverse Transcription PCR (RT-PCR), RNA can be amplified and the amount of messenger RNA (mRNA) can be determined in the sampled tissues, providing an accurate index of the activity of the parent gene. From this index, it is possible to infer many aspects of the physiological status of the organism, including reproductive and nutritional parameters (Morin and Woodruff 1996).

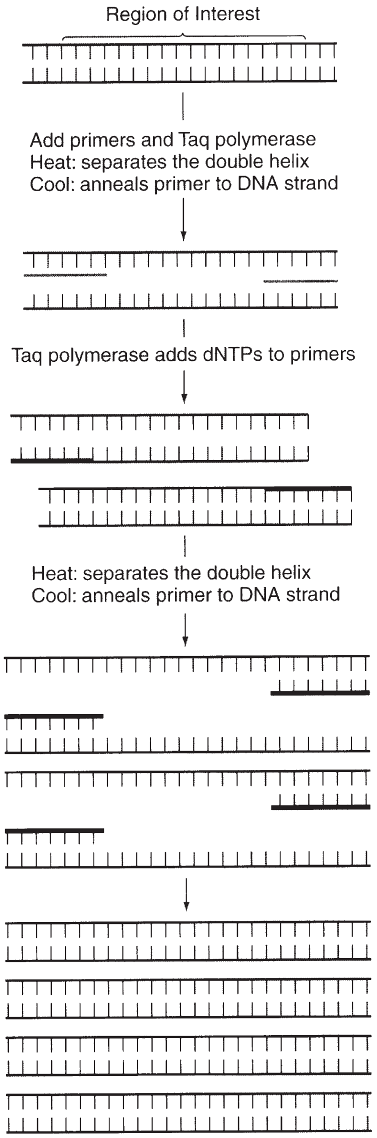


FIGURE 7.2. A schematic representation of the mechanism for a polymerase chain reaction (PCR). PCR is a technique that is used to multiply (i.e., amplify) the amount of DNA of interest. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications.* Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

7.2.4. Random Amplified Polymorphic DNA (RAPD) Analysis

A different genetic analysis technique, but one that makes use of PCR, is the ***Random Amplified Polymorphic DNA (RAPD) analysis***. In RAPD, only a single random oligonucleotide primer is used. RAPD can generate essentially unlimited numbers of loci for analysis. Only a small amount of tissue is needed, and it can be stored indefinitely after sampling and prior to analysis. The same DNA primer can be used on any organism (Fritsch and Rieseberg 1996). What renders the RAPD technique useful to conservation biologists, particularly in field studies, is that it is a noninvasive sampling technique. Small amounts of discarded hair, feathers, feces, urine, fins, scales, antlers, or other material can be used without capturing or handling the organism (Morin and Woodruff 1996). The analysis can be used even with DNA from materials that animals have chewed and then spat out (Inoue and Takenaka 1993; Takenaka et al. 1993).

PCR and RAPD analyses also have important applications in phylogenetics. The banding pattern observed in RAPD analysis, for example, when the products are subjected to electrophoresis, is a reflection of sequence variations of the template DNA taken from the sample. Differences in sequence variation of two or more individuals can be assessed for relatedness because closely related organisms would be expected to have banding patterns more similar than distantly related organisms. In RAPD, the banding patterns can be broadly classified into two groups: variable (polymorphic) and constant (nonpolymorphic). Products that qualify as constant or variable are relative to the taxonomic group. For example, an RAPD analysis can identify certain fragments that are always the same for all species within a genus, but other fragments that differ among species. Similarly, some fragments are the same for all populations within a species, but other fragments differ among populations. The variable fragments can be used to make a positive identification of the species or population that contributed the genetic material (Hadrys et al. 1992). This technique is a powerful and increasingly common tool in resolving taxonomic and phylogenic ambiguities in related species or in identifying relatedness of different populations. Such analysis enables conservation biologists to become more certain in determining which populations and taxa to manage and protect. Because PCR and RAPD can be used not only on tissues from living organisms, but even from those long dead, such as museum specimens, it provides a means to compare past populations to current ones, as in the case of the Mauritius kestrel discussed in Chapter 6. Because of their abilities to clarify taxonomy and phylogeny, PCR and RAPD have played an important role in many conservation studies concerned with taxonomic relatedness and hybridization, including the previously discussed studies evaluating the comparative genetics of gray wolves, red wolves, and coyotes in historic and extant populations, including past and current levels of hybridization and introgression (Wayne and Jenks 1991; Roy et al. 1994). Such analyses can be taken a step further to determine paternity and kinship relationships as well because RAPD markers can be treated like Mendelian alleles, and then used in single-locus "fingerprint" profiles to determine, with a high degree of probability, the genetic relatedness between individuals (Hadrys et al. 1992) (Figure 7.3), a technique with increasingly wide application in conservation biology.

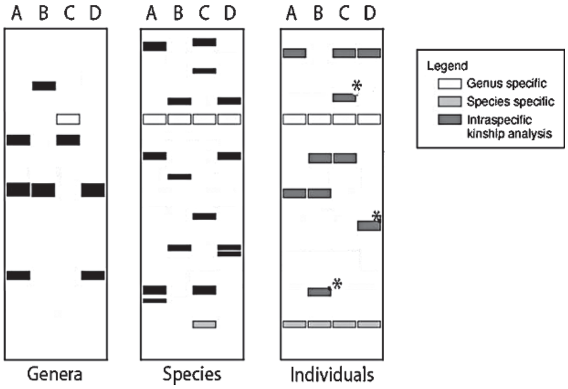


FIGURE 7.3. An example of the use of polymorphic and nonpolymorphic RAPD fragments to achieve different levels of taxonomic resolution. In the left figure, the presence of a genus-specific band identifies individual C as a member of a particular genus. In the middle figure, all individuals have the same genus band, but individual C has a species specific fragment that identifies it as a member of a particular species. In the right figure, three polymorphic fragments (indicated with*) can be used to distinguish different individuals of the same species. (Illustration by M. J. Bigelow.)

7.2.5. DNA Fingerprinting: The Use of Satellite Markers

7.2.5.1. Minisatellites and Microsatellites – What Are Satellite Markers?

Many sections of an organism's genome consist of short sequences of DNA that may be repeated up to one million times. Such segments often have different sequences of bases than other forms of DNA, and therefore different molecular densities. These repetitive sequences are known as "***satellite DNA***" (Sudbery 1998).

Some types of satellite DNA are interspersed throughout an organism's genome. There are two classes of such DNA, ***minisatellites*** and ***microsatellites***. Larger minisatellites consist of 10–100 base pairs repeated in tandem arrays that vary in size from 0.5 to 40 kb (kb stands for "kilobase," a unit of 1,000 base pairs). Some of the loci on homologous chromosomes within minsatellites are highly variable in

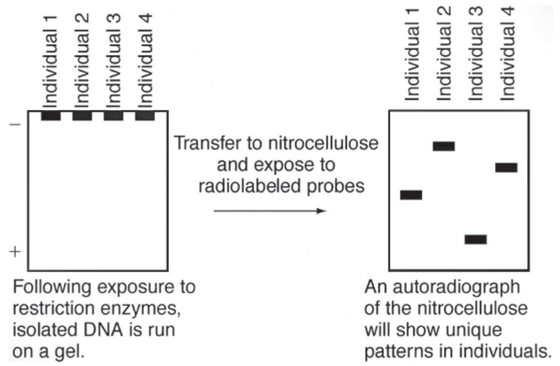


FIGURE 7.4. A schematic example of a DNA "fingerprint" produced by fractionation of different bands of DNA associated with microsatellite markers. Restriction enzymes cut the DNA at specific sequences. The amount of DNA between sequences differs between individuals; therefore, unique patterns will appear. Because DNA has a slight negative charge it will move towards the positive electrode. Smaller pieces move faster and are found near the base of the gel. This process is referred to as fractionation using gel electrophoresis. Following separation, the DNA double strands are denatured to single strands using heat or chemical treatment. A DNA print of the gel is transferred and fixed onto nitrocellulose paper. The single stranded DNA is subjected to a probe specific for a gene within the microsatellite. Unique binding patterns of the radioactive probe can be observed using autoradiography. (Illustration by M. J. Bigelow.)

length. Hence, minisatellites also are referred to as variable number tandem repeats (VNTR), and their variability forms the basis for DNA fingerprinting (Figure 7.4). Differences in length are unique to individuals, thus providing a basis for certain identification.

Compared to minisatellites, microsatellites are smaller, consisting of short tandem repeats (STRs) only two to four nucleotides in length (Sudbery 1998). Like minisatellites, microsatellites are polymorphic and provide valuable genetic markers, but they have a more uniform distribution in the genome. This makes them especially helpful in determining pedigrees of individuals and in forensic applications to determine the origin of individual animals or wildlife products. Microsatellites also can be evaluated with less expensive and labor-intensive techniques. The high variability of mini- and microsatellite markers makes both useful for many applications in conservation because allozyme (protein-coding) DNA markers are often invariant in many species (Hedrick 1999).

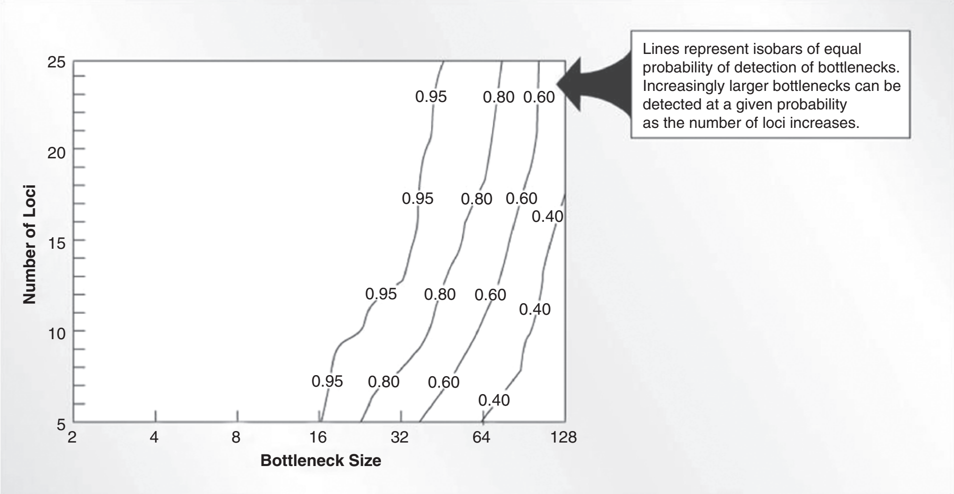
7.2.5.2. Measuring Genetic Diversity with Minisatellites and Microsatellites

Although valuable in distinguishing genetic differences among individuals and populations, minisatellite and microsatellite DNA analysis must be interpreted with caution. The high variability that gives mini- and microsatellites an advantage over allozyme markers can also lead to serious errors of interpretation. Precisely because both mini- and microsatellites usually possess very high within-population heterozygosity, the magnitude of differentiation measured between populations may be small. For example, the commonly used value of allelic differentiation in alleles among multiple subpopulations, G_{ST}, can be quite low because it is derived from the difference between the proportion of heterozygous individuals in the population (H_T) and the averaged weighted heterozygosity within subpopulations (H_S) divided by H_T. In other words,

$$G_{ST} = \frac{H_T - H_S}{H_T}.$$

If both H_T and H_S are large (and they can be if measured with micro- or mini satellite DNA), then the value of G_{ST} will be small. Thus, the method can give a false impression of low genetic variability within the population. The same problem also occurs with other commonly used measures of genetic variability in populations (Hedrick 1999), so measures chosen to estimate differences should be variation independent (Hedrick 1999). A second problem with satellite DNA is that bottlenecks can generate large genetic distances in a short time in these loci. Mini- and microsatellite data from two populations can be used to estimate time since divergence because genetic distance is assumed to increase linearly with time since divergence (Nei 1972). However, if one or both of the groups have gone through a substantial reduction in population size, the amount of genetic distance may increase very quickly and the observed genetic distance may not accurately reflect time since divergence. The problem is accentuated in comparisons of multiple groups (three or more populations) if those populations have experienced historic differences in effective population size. The problem can be avoided by using statistical tests for genetic data that have been developed for determining whether or not a bottleneck has occurred (Cornuet and Lukart 1996).

A third problem is perhaps the most basic and important of all: genetic markers are indices of genomic variation, and the genes they contain are not necessarily the ones that are the most important targets of natural selection, or the most important determinants of an organism's fitness (O'Brien 1994). In other words, the patterns of variability present in the most adaptive loci (i.e., loci that exert more direct influence on fecundity and survival) may not be closely correlated with variability in the highly variable loci of minisatellites and and microsatellites (Hedrick 1999). Practically, this means that statistically significant differences in genetic data associated with satellite markers may have little biological significance. To avoid this problem, Hedrick (1999) recommends using tests of statistical power to evaluate a known biological effect. For example, one can determine the relation between the



Lines represent isobars of equal probability of detection of bottlenecks. Increasingly larger bottlenecks can be detected at a given probability as the number of loci increases.

FIGURE 7.5. Number of loci and statistical power may be used to detect bottlenecks of different sizes. As the number of loci increases, statistical power increases. As the size of the bottleneck increases, the statistical power decreases. As both the number of loci and the size of the bottle neck increase, statistical power increases. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications.* Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

number of loci needed for evaluation to detect bottlenecks of different sizes at different levels of probability. This relation can be seen in Figure 7.5 where each of the curves displayed represents a statistical "isobar" of equal probability of detection for a combination of number of loci and bottleneck size. For example, with only five loci, the probability of detecting a population bottleneck of 30 is less than 0.80. But if the number of loci is increased to 20, the probability of detecting a bottleneck of the same size increases to more than 0.95. Such an analysis demonstrates that it is relatively easy to detect statistical significance in bottlenecks of larger population sizes if many loci are evaluated. However, if such bottlenecks last only one generation, they might have little biological significance.

Alternatively, there may be a lack of statistically significant differences in satellite DNA even when there is a biologically meaningful difference between groups. Hedrick (1999) notes that Scots Pine (*Pinus sylvestris*) in Finland shows no significant genetic distance differences when satellite markers are assessed between northern and southern populations, yet these populations differ in several adaptive traits and do not transplant well from one region to another. Another error arises when there are statistically significant differences between genetic markers in populations, but no measurable adaptive differences. This is a particular problem in cases with highly polymorphic loci where small differences may be statistically significant but not affect adaptive traits.

To solve these kinds of problems, analyses of satellite markers should be complemented with analyses of allozyme markers that are more likely to include genetic material more closely correlated with fitness. However, future advances in genetics may solve this problem in a more meaningful way. Just as the Human Genome Project is now successfully mapping the location of every human gene and determining its function, so concurrent research is now mapping the genomes of other species, especially mammals. Such research has revealed many similarities in basic organization and a highly conservative genetic structure among mammals. Thus, geneticists may one day map the genomes of other non-human organisms, perhaps including those most imperiled with extinction, using the human genome as a starting point (O'Brien 1994).

7.2.6. Mitochondrial DNA

Mitochondria are organelles found in all eukaryotic cells that function primarily in converting chemical energy into energy that can be used directly by the cell. Unlike most other organelles, mitochondria have their own, non-nuclear complement of DNA. Each mitochondrion contains between two and ten copies of a circular genome, much smaller than the corresponding nuclear DNA genome. This mitochondrial DNA (mtDNA) is specific for particular cellular functions associated with the mitochondria, including the synthesis of subunits that function in cellular respiration, units that code for the synthesis of the transfer RNA (tRNA) of each amino acid, and DNA involved in the synthesis of ribosomal RNA (rRNA) that functions in protein synthesis (Figure 7.6).

mtDNA also is unique in that it is maternally inherited as a linked set of genes, passed on to progeny in the cytoplasm of the egg cell (Cronin 1993; Sudbery 1998). Thus, there is no recombination between maternal and paternal genomes. This mode of inheritance results in rapid mtDNA differentiation relative to nuclear genes and makes the construction of phylogenetic trees straightforward because, without recombination, the number of nucleotide differences between the mtDNA genomes of different individuals, populations, or species can be assumed to be a direct measure of phylogenetic relatednesss (Sudbery 1998). Theoretically, phylogenies derived from mtDNA are not affected by historic changes in effective population sizes, unequal sex ratios, or unequal family sizes. Many

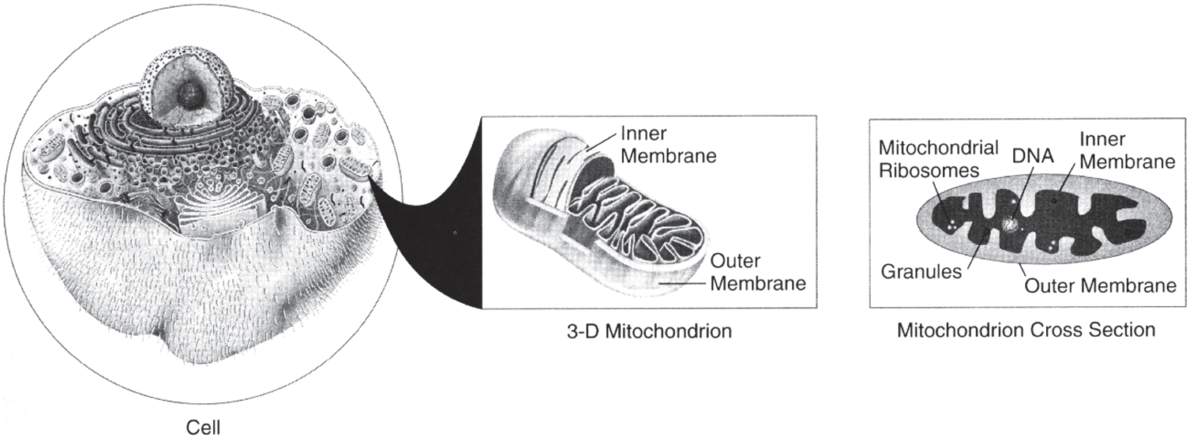


FIGURE 7.6. A schematic diagram of a loop of mitochondrial DNA. Unlike nuclear DNA, mitochondria DNA is not enclosed within a membrane. Rather, it is found within the matrix of the organelle. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications.* Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

taxonomists consider phylogenetic analysis of mtDNA to be a superior, more objective method of determining phylogeny because it is based entirely on quantitative characters. Because it is maternally inherited, mtDNA can be used to determine a maternal lineage in an individual or group, but not a paternal one.

The small size of the mtDNA genome means that its sequences have long been known, and it is easy to identify polymorphisms in it. This trait is complemented by the fact that certain regions of mtDNA evolve at faster rates than single-copy nuclear genes in mammals (Wilson et al. 1985), so they can be especially useful for studying differences at the population level. The mtDNA molecule as a whole evolves at a rate of about 2% per 1,000,000 years, but some areas on the molecule can change at up to five times this rate (Greenberg et al. 1983; Cann et al. 1987). Overall, mtDNA evolves five to ten times faster than nuclear DNA, and permits studies of recent evolution that nuclear DNA would not record. Protein electrophoresis and restriction enzyme analysis can both be applied to mtDNA.

As powerful, and as useful, as mtDNA analysis can be in conservation biology, it is critical to remember that mtDNA provides information only on maternal descent. As we shall see in a subsequent case history (Karl et al. 1992), the absence of paternal influence on mtDNA can lead to erroneous conclusions in populations that are sexually structured genetically or sexually segregated, or where different sexes make unequal contributions to gene flow between population subunits. A second caution in interpreting mtDNA data is to remember that mtDNA normally evolves independently of and at a much faster rate than nuclear DNA. Finally, mtDNA may not be as closely correlated to the organism's fitness or its true phylogenetic divergence from other populations as nuclear DNA.

Similarities and differences in mtDNA do not always correlate with other taxonomic criteria. Some related species and subspecies have phylogenetically distinct mtDNA, but others known and recognized as separate species show little or no divergence in mtDNA. Cronin (1993) notes that, among North American cervids, the mule deer (*Odocoileus hemionus hemionus*) has mtDNA that is divergent from its conspecific subspecies, the Sitka black-tailed deer (*O. h. sitkensis*) and the Columbian black-tailed deer (*O. h. columbianus*), but not distinct from a different species, the white-tailed deer (*O. virginianus*). Likewise, there is more similarity of mtDNA in brown bears (*Ursus arctos*) and polar bears than among geographic races of brown bears, and, among North American waterfowl, there is more similarity between some populations of mallards (*Anas platyrhynchos*) and black ducks (*Anas rubripes*) than among different populations of mallards. No one would seriously propose, however, that brown bears and polar bears, or mallard ducks and black ducks, be classified as the same species, receive the same management treatments, or be subject to the same conservation strategies. Thus, these cases suggest that mtDNA alone might not provide a sufficient assessment of overall genetic differentiation, but rather should be used for taxonomic classification only when it can be complemented by an analysis of other, nuclear genetic material (Cronin 1993). The variable mtDNA genotypes in ancestral populations may be sorted independently in descendent populations, some of which may differentiate into new species, although others may not. After speciation, nuclear genes in the two groups may diverge greatly, but ancestrally shared mtDNA genotypes may not. As a result, perfectly recognizable and distinct species may have nearly identical mtDNA sequences. As conservation biology continues to use genetic techniques as a basis for determining strategies for conservation, care and discernment are needed to ensure that the power of a genetic technique does not run ahead of sound biological judgment.

7.2.7. Restriction Fragment Length Polymorphism (RFLP): A Technique for Assessment of Genetic Variation Among Individuals

To measure variations of nuclear DNA among individuals, one of the most common and effective techniques is that of ***Restriction Fragment Length Polymorphisms*** or RFLPs, which are variations in the length of restriction fragments produced from identical regions of the genome (Lodish et al. 2000). Variations in DNA sequence (DNA polymorphisms) may create or destroy restriction-enzyme recognition sites. As a result, the patterns of restriction fragment lengths produced from exposure to restriction enzymes may vary in homologous chromosomes among individuals. To detect the differences, a radioactive marker (probe) is used to bind to the restriction site to detect the presence of the fragments. If there are no differences in the sequences of two homologous chromosomes in a particular DNA region, a restriction enzyme that binds to that region will produce fragments of identical length and sequence, and the probe will recognize this as a single fragment that will appear as one band (the restriction site occurs at the same place in both chromosomes). However, if a mutation has occurred that has destroyed a recognition site for a restriction enzyme in one individual compared with another, fragments of differing lengths will be produced, and these will be recognized as different fragments by the marker and appear as two bands (Figure 7.7).

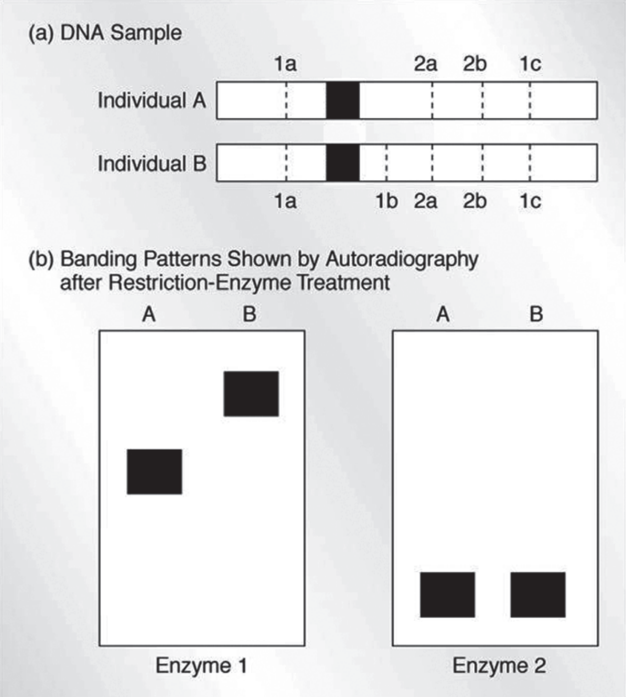


FIGURE 7.7. A schematic diagram of a RFLP result. The dark black band shown in the DNA samples represent the area to which a radioactive probe will bind. One of the restriction-enzyme recognition sites for enzyme #1 is mutated in individual A. As a result, different banding patterns will appear when the radioactive probe is measured with autoradiography. Treatment with enzyme #2 gives the same pattern in both individuals because they have identical restriction-enzyme recognition sites for enzyme 2. (Illustration by M. J. Bigelow.)

Although there are many regions of an organism's genome that are identical and repetitive, there are also regions of DNA in multiple parts of the nuclear genome that are represented only once or, at most, a few times. This kind of DNA is called single-copy nuclear DNA or scnDNA. scnDNA can be amplified by polymerase chain reactions (PCR), as described earlier, at specific loci and then digested with enzymes to produce restriction fragments. These fragments can then be separated into visually detectable bands using electrophoresis via staining. Polymorphisms among scnDNA segments are numerous, and their Mendelian inheritance can be determined via pedigree analysis because they are a form of nuclear DNA, not mtDNA. Thus, scnDNA can provide a wealth of genetic markers that can be used to estimate genetic diversity in a population (Loew 2002:234). scnDNA has been used in a variety of conservation studies, including studies of the endangered green turtle (Karl et al. 1992). In this species, initial genetic studies of maternally-inherited mtDNA suggested a highly substructured population with high genetic variation and little gene flow between breeding areas. Using scnDNA analysis, researchers determined that there was only modest population substructure, with moderate rates of male-mediated gene flow. In other words, the scnDNA study revealed that gene flow was higher than previously supposed, and that it occurred primarily through male turtles, who were less likely to mate in only one breeding area (Karl et al. 1992). These insights could not have been gained from mtDNA analysis alone, and this study illustrates the aforementioned need to complement mtDNA analysis with analysis of nuclear DNA to reach valid conclusions and insights about population processes, genetic structure, and reproductive ecology.

POINTS OF ENGAGEMENT – QUESTION 1

Can you identify a problem that a particular molecular genetic technique allows a conservation biologist to ask that, prior to that technique's development, could not have been asked? What value is added to a conservation effort by being able to ask and to answer the question you have identified?

7.3. Captive Breeding: Managing Genetics of Captive Populations

7.3.1. Using Genetic Techniques to Recover Genetic Diversity and Population Size in Captive Populations: The Historical Background

Because of the many difficulties and uncertainties facing *in situ* populations, captive-breeding programs – particularly those associated with zoos – may be the last best hope for many endangered species. Over 25 years ago conservation geneticist William Conway summarized the role and purpose of captive breeding programs in conservation with an almost brutal frankness. "Captive propagation has had a simple-minded directness: an immediacy that offers attractive reinforcement to the complex geo-political tasks of habitat preservation. It has been a kind of 'ark.' Such programs pretend to offer no overall cure for the epidemic of extinction but provide topical treatments of the symptoms expressed by the loss of higher animals. Simply expressed, captive propagation offers another way of fighting the continuing reduction of earth's diversity – an opportunity to preserve options" (Conway 1980).

The concept of zoos as a genetic "ark" is increasingly complemented in modern conservation biology by the growing role of zoos as institutions of genetic research and management. The "topical treatments" of captive breeding programs that Convay referred to over 25 years ago have taken a variety of forms in contemporary conservation biology. But, for all their diversity, they are uniform in their pursuit of four primary conservation functions. These programs are designed to provide: (1) substitutes for wild individuals and populations that can be used in basic biological research, (2) opportunity for the development of care and management techniques, (3) demographic and genetic reservoirs that will augment existing wild populations, and (4) a remnant of those species for which there is no immediate opportunity to survive in the wild (Conway 1980).

7.3.2. Solving the Fundamental Problem: Minimizing Adaptation to Captivity

Historically, breeders have used various strategies to manage captive populations for various goals. "Active breeding" is one of the oldest. In this strategy, breeders brought the "best" animals together for mating or used those that simply bred on their own, assuming that breeding animals were the fittest individuals. But "best," in captivity, often translated into the most docile animals or those that quickly adapted to a captive environment. Neither trait adds to the survivorship of wild populations. As an active selection strategy was repeated in subsequent generations, it led to increased inbreeding, loss of genetic variability, and fixation of traits adaptive for captivity, but not for life in the wild. In his analysis of a failed attempt to establish a population of hybrid domestic X wild turkey (*Meleagris gallopavo*) in Missouri (USA), Aldo Leopold attributed the failure to specific differences in behavior between the hybrid turkeys (raised in captivity) and wild turkeys. He noted that the domestic turkeys were more docile, bred earlier in the season, and that the chicks scattered when the hen sounded a note of alarm. Chicks of wild turkeys hide. Commenting on this failure, Leopold remarked, "Wild turkeys are wary and shy, which are advantageous characteristics in eluding natural and human enemies. They breed at a favorable season of the year. The hens and young automatically react to danger in ways that are self-protective. Reproductive success is high.… Birds of the domestic strain, on the other hand, are differently adapted. Many of their physiological reactions and psychological characteristics are favorable to existence in the barnyard but may preclude success in the wild" (Leopold 1944). Such attempts at turkey reintroduction using captive-raised turkeys were repeated widely throughout the United States. With the exception of northern Michigan where a domestic-raised population did establish itself in the wild, all efforts were unqualified failures.

The problem Leopold described in turkeys is present in every captive population. It is the problem of adaptation to captivity. The more accustomed and well-suited wild animals become to their environment in captivity, the less likely they may be to survive if returned to an environment in the wild. The genetic adaptation to captivity, which we will call *GA*, can be described mathematically in this expression:

$$GA \sim \frac{Sh^2}{L}\sum_{i=1}^{y/L}[1-1/(2N_e)]^{y/L}(1-m_i),$$

where S is the selection differential in captivity (i.e. the strength of selection for captive traits) and h^2 is heritability (additive genetic variation for reproductive fitness). y/L is the number of generations in captivity (expressed in years (y) per generation length (L)). N_e is the (by now familiar) effective population size, and m_i is the proportion of genetic material derived from immigrants (new animals) in the ith generation.

Although at first glance an intimidating equation, we can begin to understand the relationship and its application by concentrating first on the goals of a conservation biologist working as the captive breeding manager. The goal of the conservation biologist is to reduce the value of *GA* to the lowest possible level. Look at the equation again and consider what the biologist could do to minimize the value of *GA*. The biologist could

1. Reduce the amount of time in captivity (reduce the number of iterations of $\sum_{i=1}^{y/L}$)
2. Reduce the strength of selection in captivity (the value of S)

3. Equalize family sizes, so that selection occurs only within families
4. Add more immigrants (unrelated individuals) from wild or captive populations to slow the rate of genetic adaptation

Action 3, equalizing family size, should reduce selection for captivity (a way of implementing Action 2). At an experimental level, Frankham (2005) found that equalizing family sizes in fruit flies did yield the expected reduction in the strength of selection for captivity, but "produced little improvement in reintroduction success" and did not prevent "substantial adverse effects upon reintroduction into the 'wild' from benign captive conditions …" (Frankham 2005:753).

Although it is increasingly difficult and discouraged in conservation today to implement Action 4 by capturing more wild individuals to augment captive populations, "immigrants" to a particular captive population need not come from wild stocks. With increasingly coordinated and well-designed captive breeding management plans that involve the transfer of animals from one zoo to another, animals from one region can act as founders to other regions to which they are exchanged. Understanding the intention, methods, and scope of such management plans is essential if we want to grasp the way in which captive populations are integrated into worldwide conservation strategies today.

7.3.3. Captive Breeding Today

Today captive breeding efforts are no longer the haphazard, often fortuitous adventure that was characteristic in past times. They now are highly coordinated, international scientific initiatives using careful records of past mating events and high levels of scientific technology and expertise for planned present and future breeding. In 2007, the Association of Zoos and Aquarium was coordinating breeding and management plans for approximately 350 species in captivity, and more continue to be added. We must note that many captive management programs are in place simply to supply individuals of particular species to existing zoos and other facilities without further impact on wild populations. "Maintenance" oriented programs like these do not always involve endangered species and may never have a role in the recovery of wild populations, but, on the other hand, we cannot predict with certainty where, when, and in what populations recovery might someday be needed. For example, most of the world's captive polar bear population was founded with rehabilitated specimens from wild populations who were removed from the wild because of conflicts with humans. There was never any intent to use such individuals in "conservation" beyond the educational benefits of exhibiting polar bears to the public. Today, as global climate change is reducing available arctic sea ice and contributing to reductions in wild polar bear populations (Chapter 5), such captive individuals in zoos may yet become a valuable resource in conservation for someday helping decimated wild polar bear populations recover from the current reductions they are now experiencing.

Most captive populations are being managed for maintenance and possible recovery in the wild according to principles of population genetics and demography. Many of these are so-called "closed populations," which must be managed to be self-sustaining in captivity with no further inputs from wild stock, and no plans for return to the wild, for the foreseeable future. The goals of breeding programs for such populations are to minimize changes in the genetic constitution of these populations (i.e. preserve the original level of genetic diversity), to mitigate problems associated with inbreeding depression, and to reduce adaptation to the captive environment (i.e. to retain "wildness" in the captive population). The first and third goals look ahead to a day when offspring of captive individuals may be reintroduced into the wild to augment natural populations. To have hope of success, such individuals must retain as much genetic diversity as possible from their wild-caught ancestors to cope with natural (and unfamiliar) environments. The second goal, reduction of inbreeding depression, is aimed at maintaining high survivorship and vitality among captive populations as long as they remain in captivity.

Carefully planned, globally coordinated strategies of captive breeding may lead to reintroduction in the wild at some future time to supplement existing wild populations or establish new ones (Hedrick and Miller 1992). This strategy has taken the form of the Species Survival Plan (SSP) and Population Management Plan (PMP) programs in North America, and their counterparts in Europe, the European Endangered Species Program (EEP) and European Studbook (ESB), all of which are cooperative management programs in which zoos coordinate captive breeding efforts for hundreds of species.

Detailed information on each species is kept in databases called "studbooks," which contain all known information about each individual in the captive population, including its relationships to other captive individuals. Studbooks provide the data for ***pedigree analysis***, which enables managers to determine the kinship of individuals to one another in a captive population and evaluate the breeding priority of particular individuals and plan mating strategies that minimize inbreeding and conserve genetic diversity. Knowing kinship, mangers can design more complex breeding strategies that minimize inbreeding, maximize retention of genetic diversity, and minimize relatedness of individual mating pairs. To see how such analyses can inform the breeding management plan, consider the example of one species and its management in captivity.

7.3.4. Conservation Implications of Captive Breeding – The Example of the Okapi

7.3.4.1. The Significance of the Captive Okapi Population

The okapi (*Okapia johnstoni*) easily could be the poster species for global captive breeding efforts. Considered the closest living relative of the giraffe (*Giraffa camelopardalis*), the okapi was not described by the scientific community until 1899. Inhabiting only mature, tropical moist forests in Africa, all wild populations of okapi today live within a single African nation, the Democratic Republic of Congo (DRC, formerly Zaire). Although several large reserves were established in the DRC, including four World Heritage sites, enforcement of reserve boundaries and protection of species within the reserves has never been secure. The reserves were vulnerable when they were established, and the situation grew worse due to high levels of human population growth and immigration of refugees into reserves and surrounding areas (Wilkie and Finn 1990; Hart and Hall 1996; Wilkie et al. 1997). Okapi populations declined as a result of slash-and-burn cultivation and subsequent forest succession associated with human population growth (Wilkie and Finn 1990). To make matters worse, the government of the DRC has been destabilized by civil war and the incursions of neighboring countries, which have backed rebel forces. For several years, rebels held the eastern portion of the DRC, where the reserves are located. The headquarters of three of the four World Heritage sites were looted, and all technical equipment and vehicles were stolen. Some park guards were killed (Hart and Hart 1997). In the face of such instability, conservation funding from western organizations declined (Hart et al. 1996). Open hostilities in the civil war came to an end in 2003 and the country is moving toward political stability, but the conservation effort in the DRC remains uncertain, especially regarding the protection of existing parks and the okapi populations within them.

The okapi has thrived in captivity, enjoying longevity and high fecundity. Thus, okapis are now well represented in zoos around the world. The okapi studbook database is kept at the Antwerp (Belgium) Zoo, one of the world's oldest and most famous zoological gardens, and where okapis were first bred in captivity (Figure 7.8). Data from the okapi studbook have been used to develop a worldwide okapi managed breeding program that identifies the breeding priority of each individual, minimizes inbreeding, and mitigates loss of genetic diversity in the captive population. To begin, consider how to use these data to conduct a pedigree analysis.

FIGURE 7.8. The female okapi "Lieve," studbook number 328, a member of the captive okapi population at the Antwerp Zoo in Belgium where the world's okapi studbook database is kept. The honor is fitting for the Antwerp Zoo as it was the world's first zoo to successfully maintain the okapi in captivity. Studbook data, such as those kept at the Antwerp Zoo, are used to develop pedigree analyses for worldwide captive breeding programs for many species. Today matings of animals in captive populations, like Lieve, are carefully planned and recorded for use in ongoing pedigree analysis of captive populations. Studbook data are used to identify the breeding priority of each animal, minimize inbreeding, and reduce loss of genetic diversity in the managed captive population. (Photo courtesy of Patrick Immens, Antwerp Zoo, Belgium.)

7.3.4.2. Pedigree Analysis and Kinship

Using studbook data, pedigrees can be created to track relationships among family members, both living and historical. A pedigree tracks a group of unrelated individuals (founders) that form a new population and their descendants each generation through the last living individual. A simple pedigree analysis might look something like Figure 7.9.

If you wished, you could draw a pedigree for the okapi group shown in Table 7.1. You would use circles to represent females (dams) and squares to represent males (sires), and then connect related individuals with lines as in the previous figure. Individuals with "WILD" parents are founders originating from wild or other unrelated populations. Founders are assumed to be unrelated to one another, and the same is assumed of wild parents unless data, such as molecular data or capture records, suggest otherwise, in which case known relationships could be inserted into the "founder" matrix.

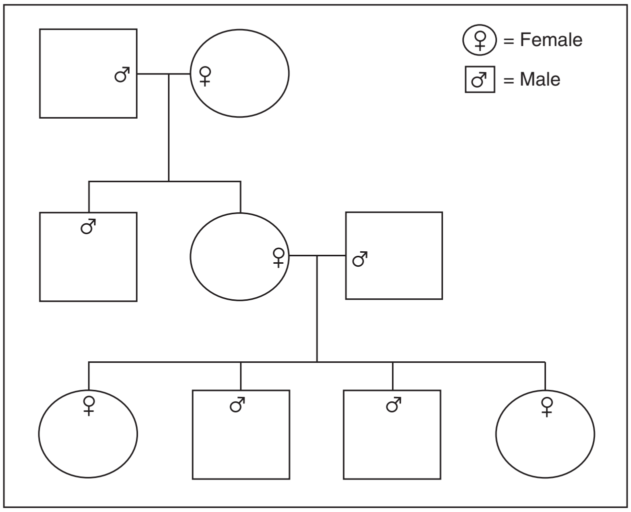


FIGURE 7.9. A generalized example of a simple pedigree diagram. Squares represent males and circles represent females. In this example, the parents (wild-caught founders) produce a male and a female offspring. The male offspring does not mate, but the female mates with an unrelated male (avoiding inbreeding) to produce four offspring – two males and two females. (Fred Van Dyke, *A Workbook in Conservation Biology: Solving Practical Problems in Conservation.* Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

TABLE 7.1. A captive ten-member okapi (*Okapia johnstoni*) group consisting of four wild-born founders (okapi 47, 71, 85, and 100) and their six descendants. Such information can be used as a basis to begin a pedigree analysis of a captive breeding group.

ID	Sex	Dam	Sire
71	Male	Wild	Wild
85	Female	Wild	Wild
47	Male	Wild	Wild
100	Female	Wild	Wild
160	Female	85	71
181	Male	85	71
196	Female	85	71
198	Male	100	47
253	Female	160	198
258	Male	196	198

Source: Data courtesy of K. Leus.

Knowing the ancestry of all individuals in a population allows managers to calculate kinship. As a result of the nature of the nature of Mendelian genetics and the independent assortment of chromosomes during sexual reproduction, we can measure the kinship between two individuals with simple probabilities. A ***kinship coefficient*** (k_{ij}) between two individuals (i and j) is the probability that alleles randomly selected from homologous loci in two individuals are identical by descent from a common ancestor.

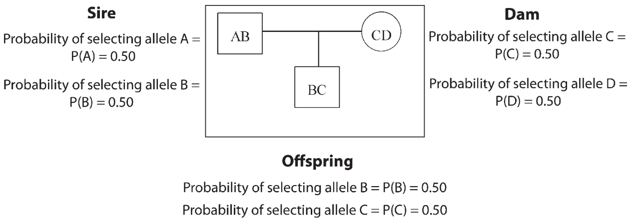


FIGURE 7.10. Diagrammatic representation of kinship (k) between parents and their offspring. Letters in boxes represent alleles of each individual. (Fred Van Dyke, *A Workbook in Conservation Biology: Solving Practical Problems in Conservation.* Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

To determine what these kinship probabilities are, start from the fact that a diploid organism inherits one-half of its alleles from its mother and one half from its father, so that is has two alleles for each gene locus (Figure 7.10, alleles B and C in offspring). Thus, the probability of selecting one particular allele (for example, B) of the two possible in any diploid organism is 50% (0.50), the same odds as getting either heads or tails if flipping a coin. If one were randomly sampling alleles from homologous loci of an individual and one of its parents, the probability of selecting a particular allele (for example, B) would be equal to the product of the two individual probabilities (0.50 chance of choosing B from the offspring × 0.50 chance of choosing B from a parent = 0.25) This calculation reveals that there is a 25% probability that alleles selected from an offspring and its parent would be identical by descent from a common ancestor. Therefore, the kinship between a parent and offspring is 0.25.

In this example, the offspring share one allele with the sire and one allele with the dam. The kinship (k) of the sire with the offspring is equal to the probability of selecting the B allele in the sire times the probability of the selecting the B allele in the offspring or

$$P(B)_{\text{sire}} \times P(B)_{\text{offspring}} = 0.50 \times 0.50 = 0.25.$$

Similarly, the kinship of the dam with offspring is equal to

$$P(C)_{\text{dam}} \times P(D)_{\text{offspring}} = 0.50 \times 0.50 = 0.25.$$

Thus, you can see that sibling-offspring kinship is normally a value of 0.25. Some other common kinships in a typical pedigree might include:

Relationship	Kinship
Parent–offspring	0.25
Sibling–sibling	0.25
Grandparent–grandoffspring	0.125
Half-sibling–half-sibling	0.125
Uncle/aunt–nephew/niece	0.125
Cousin–cousin	0.0625
Second cousin–second cousin	0.03125
Unrelated	0

7.3.4.3. Population Mean Kinship

Once we determine an individual's kinship to all other individuals in a population, a mean kinship for that animal can be calculated. ***Mean kinship*** (mk) is the average of the kinships between a single individual and all other individuals in the population. Mathematically, it can be expressed as

$$\sum_{j=1}^{N} mk_i = k_{ij}/N,$$

where mk_i is the mean kinship of the *i*th individual, k_{ij} is the kinship of individual *i* to individual *j*, and *N* is the number of individuals in the population. Thus, every individual (in this case, every okapi) would have its own *mk* and its own *k* to every other individual. To extend the value of the original pedigree analysis, the values of *mk* for every pairwise combination of individuals in the captive population could be recorded in a matrix configuration like the one in Table 7.2.

Just as we can determine the mean kinship of individuals to one another, we also can find the average kinship value of the population, or the ***population mean kinship***. Population mean kinship is simply the arithmetic mean of all the individual mean kinships, as calculated in the previous expression. An individual whose mean kinship is less than the population mean kinship has fewer relatives in the captive population than an individual whose mean kinship is greater than the population mean kinship.

The population mean kinship (*MK*) can be calculated as

$$MK = \Sigma mk_{\mathrm{i}}/N,$$

where mk_i is the mean kinship of the *i*th individual.

7.3.4.4. Relationship of Inbreeding to Kinship

Another genetic metric that can be calculated in a pedigree analyses is an individual's inbreeding coefficient (*F*), defined and calculated previously. Inbreeding, or the mating of relatives, is a concern to genetic management because it reduces variation. As we have noted in Chapter 6, inbred individuals have a higher probability of being homozygous (having identical alleles at a genetic locus), and often have higher mortality rates and reduced fecundity compared to non-inbred individuals. Whereas managers of wild populations must be primarily concerned about threats associated with environmental variation and catastrophes, mangers of captive populations must focus on avoiding genetic deterioration of the population, which can be aggravated by inbreeding.

Although we have previously introduced various expressions to calculate the value of the inbreeding coefficient *F*, we can now reveal an easier way, made possible by the data we have already analyzed in pedigree analysis and the relationship between kinship and inbreeding. The relationship is this. *An individual's inbreeding coefficient is equal to the kinship between its parents*. Thus,

$$F = K_{\mathrm{ij}}, \text{ where } i = \text{sire and } j = \text{dam}.$$

For example, if an individual's parents are completely unrelated, their kinship to one another is equal to 0; they have 0% probability of sharing any alleles that are identical by descent. Consequently, any offspring they produce would have a 0% probability of having both of its alleles identical by descent, so its inbreeding coefficient would be 0.

Calculating individual inbreeding coefficients from pedigree data is useful, but that is not all we can do. We can use the same data to determine another valuable measure of population genetics. That measure is called ***gene diversity***.

Gene diversity (*GD*) (not to be confused with the general concept of "genetic diversity") is the most commonly used measure of the level of genetic variability in a captive population, especially in zoos, by population managers. By definition, gene diversity is the probability that two alleles from the same locus sampled at random

TABLE 7.2. A matrix of kinship for each individual okapi to all other individual okapi in a breeding group. Assume that founding individuals 47, 71, 85, and 100 are unrelated to one another. To see how you could use the matrix to, at a glance, determine the kinship of any individual to every other individual, follow the row or column of bold numbers, both of which represent the kinship of okapi 160 to every other okapi in the group. To determine the individual mean kinship (mk_i) of okapi 160, sum the row or column total of its kinships and then divide by the number of individuals in the population (in this case, 1.875/10 = 0.1875).

ID	47	100	71	85	160	181	196	198	253	258	mk
47	0.5000	0.0000	0.0000	0.0000	**0.0000**	0.0000	0.0000	0.2500	0.1250	0.1250	0.1000
100	0.0000	0.5000	0.0000	0.0000	**0.0000**	0.0000	0.0000	0.2500	0.1250	0.1250	0.1000
71	0.0000	0.0000	0.5000	0.0000	**0.2500**	0.2500	0.2500	0.0000	0.1250	0.1250	0.1500
85	0.0000	0.0000	0.0000	0.5000	**0.2500**	0.2500	0.2500	0.0000	0.1250	0.1250	0.1500
160	**0.0000**	**0.0000**	**0.2500**	**0.2500**	**0.5000**	**0.2500**	**0.2500**	**0.0000**	**0.2500**	**0.1250**	**0.1875**
181	0.0000	0.0000	0.2500	0.2500	**0.2500**	0.5000	0.2500	0.0000	0.1250	0.1250	0.1750
196	0.0000	0.0000	0.2500	0.2500	**0.2500**	0.2500	0.5000	0.0000	0.1250	0.2500	0.1875
198	0.2500	0.2500	0.0000	0.0000	**0.0000**	0.0000	0.0000	0.5000	0.2500	0.2500	0.1500
253	0.1250	0.1250	0.1250	0.1250	**0.2500**	0.1250	0.1250	0.2500	0.5000	**0.1875**	0.1938
258	0.1250	0.1250	0.1250	0.1250	**0.1250**	0.1250	0.2500	0.2500	**0.1875**	0.5000	0.1938

Source: Original matrix design by S. Long.

from the population will not be identical by descent. That is, gene diversity is really another name, and another way of looking at, a concept we introduced earlier in Chapter 6, the concept of expected heterozygosity (H_e). However, if a population manager is armed with pedigree analysis data, she need not return to the theoretical calculation of H_e to determine a measure of gene diversity. The estimate is much easier because there is a simple, direct relationship between gene diversity (*GD*) and the value of *MK*, previously calculated. That relationship is

$$GD = 1 - MK$$

Now, what are the implications? If population mean kinship (*MK*) is high, then most individuals are related and gene diversity is low. Alternatively, if *MK* is low, the population contains a larger proportion of unrelated individuals and higher gene diversity.

7.3.4.5. How Can a Captive Population Manager Retain Gene Diversity?

As you learned in Chapter 6, there will be unavoidable random loss of gene diversity in a small, captive population due to genetic drift. Genetic population managers, no matter how dedicated, experienced and skilled, cannot maintain a population's overall genetic diversity (for example, its allelic diversity) in a captive environment. Despite the inevitable loss of overall genetic diversity, managers can, by focusing on maintaining the value of a single genetic metric, the previously defined gene diversity (*GD*), maintain other kinds of genetic variation collaterally through their attempts to maintain *GD*. Specifically, managers of captive populations can manipulate population characteristics that influence the *rate* at which *GD* is lost or retained. Among these characteristics are initial population size (number of founders), effective population size, target population size, population growth rate, and generation time.

Founders – Initial population size, or number of founders, can be used to estimate the gene diversity at the time of a population's founding ($GD_{t=0}$). We can express the relationship as

$$GD_{t=0} = 1 - [1/(2N)],$$

(where N = number of wild-born founders, assumed to have unique (unrelated) alleles). If a manager is starting a captive population from scratch, the larger the number of founders, the greater the initial gene diversity. A manager must realize that there is a relationship of diminishing return in initial founder acquisition because, as a population is resampled, the additional individuals collected becomes less likely to yield more new alleles. However, it still may be important to establish strategies to acquire subsequent founders to supplement variation lost to drift in the captive population over time.

Effective population size – Recall from Chapter 6 that effective population size, N_e, is the size of an idealized, randomly mating population that is subject to the same degree of genetic drift as the actual population under consideration. The relationship between gene diversity at time *t* and effective population size is

$$GD_t = 1 - 1/(2N_e).$$

As explained in Chapter 6, effective population size has multiple (but related) meanings, but managers of captive populations usually focus on the "variance effective size," an indicator of the number of breeding individuals in a population. A population's effective size is naturally smaller than its census size because many individuals in a population do not breed (e.g., are prereproductive or postreproductive), or do not breed equally. To estimate effective population size, captive population managers use the sum of the number of living males with living offspring and the number of living females with living offspring. The ratio of effective population size to census size (N_e/N) typically ranges from 0.10 to 0.50 for intensively managed captive populations (Lacy 1995).

The effective size of a population influences the rate at which gene diversity is lost. A population with a small effective population size relative to actual census population size (N_e/N ratio) loses gene diversity more quickly than an equal-sized population with a greater N_e/N ratio because individuals without offspring do not pass on their genetic variation to future generations. Thus, mangers can reduce their population's loss of gene diversity by increasing the effective population size.

Target Population Size and Population Growth – The ***target population size*** is the size at which managers attempt to maintain a captive population. This size is often determined by the amount of space available to house a zoo population. The maximum size to which a population is allowed to grow and the rate at which population growth occurs influence the retention of gene diversity. Large populations are likely to contain more variation than small populations and rapidly growing populations have more breeding individuals contributing more of their genetic variation to the next generation. If managers can accommodate a large target population size and/or a rapid growth rate, the population will retain more genetic diversity.

Mean Generation Time – An important influence on gene diversity is ***mean generation time***, the average age at which animals produce offspring. The number of generations occurring within a given number of years is proportional to the amount of diversity that will be lost over that time. A population with a short generation time will have more opportunities for loss of gene diversity during a given time period than a population with longer generation time. Thus, managers can reduce rates of loss in gene diversity by increasing the average age at which animals breed. In fact, however, generation time is rarely manipulated in actual captive populations. Although theoretically a good idea, managers generally consider the cost of losing animals to attrition prior to recruitment too high to merit the delay of recruitment.

Strategic Implications – Let us work out the implications of what we know so far, based on our knowledge of factors that influence effective population size. Because captive populations are usually small, the first objective in a captive breeding strategy is to maximize the ratio of the effective population size, N_e, to the total (census) population size, N, in order to reduce effects of inbreeding. If the ratio of N_e/N can be maximized, the influences of genetic drift and inbreeding depression can be decreased. Methods to maximize this ratio are to (1) grow the population to its captive carrying capacity (target population size) as fast as possible, (2) maximize the number of breeders in each subsequent generation, (3) equalize family sizes, (4) equalize the sex ratios of breeders and (5) reduce fluctuations in population size. Such strategies, if successful, not only maximize the N_e/N ratio, but also retain existing heterozygosity in the population.

Valuable as it may be to know these things, these techniques and considerations do not, in themselves, dictate a comprehensive overall strategy for maximizing gene diversity in a captive population. There are two reasons for this. First, not every variable that affects population gene diversity can be optimized at the same time. For example, if one lengthens generation time, the population's growth rate will slow down. It also will slow down, in fact stop, if the target population is reached quickly. This suggests the second problem: the limitations of the captive environment. In many zoos and other collections, limitations of physical space force genetic managers and planners to examine tradeoffs between the number of individuals kept in captivity, the space that can be allocated to each, and the genetic goals that are set for each. And as for the number of founders, that is usually an event long past managing. Therefore, none of the above considerations can yield a captive breeding strategy that can be applied under all conditions. Comprehensive strategies can be developed, but they require an integration of our knowledge of kinship and inbreeding that focuses on *managed matings*, not *managed population size*. Mating selection is a population process over which managers of captive populations have the greatest control because managers can determine which male and female individuals will be permitted to mate with one another. Thus, the strategies for genetic management of captive populations that we now examine focus on the process of breeding pair selection.

7.3.5. Captive Breeding Strategies

7.3.5.1. Random Mating and Avoidance of Inbreeding Strategies

Most zoo animals are not housed individually, but held and displayed in groups that approximate normal social organizations and interactions that can allow for reproduction. Selection of individuals for these reproductive units has long-term effects on the genetic status of the population and merits careful consideration. Historically, multiple strategies have been used to assign breeding pairs for the purpose of population management, with varying effects on the rate of gene diversity loss. These strategies were random mating, avoidance of inbreeding and minimization of mean kinship.

Before the advent of technology and techniques that permitted precise assessment of genetics, many captive populations in zoos and other collections were subject to matings that had little consideration of the relationships of mated animals. Males and females were often chosen at random to create novel breeding groups. This strategy has fallen out of favor, given the availability of pedigree data and computer modeling tools for population management and the need to manage populations for long-term viability.

The first systematic effort to improve the strategy of random mating was a strategy to avoid inbreeding and maximize heterozygosity. Remember that inbreeding, F, increases homozygosity in a population and reduces mean heterozygosity (gene diversity, GD) such that

$$F = 1 - GD$$

Therefore, reducing inbreeding in a captive population should, theoretically, increase gene diversity. However, such a strategy requires a substantial founder population to be successful. For example, Frankham (1995) argued that initiating populations with at least 20–30 unrelated founders was necessary to maximize initial heterozygosity. Inbreeding depression has been documented for many taxa, and, in our model species, the okapi, experience among captive breeders has suggested that survival is lower and developmental problems usually are more common in inbred okapi than in non-inbred okapi (De Bois et al. 1990) (Table 7.3). Given such concerns, breeders have often approached the creation of breeding groups with a ***maximum-avoidance-of-inbreeding (MAI) strategy***, which avoids matings between relatives. To implement the MAI strategy, managers examine the kinship between potential mates, which is equivalent to the inbreeding coefficient of potential offspring of the pair. Pairs with little or no kinship to each another (i.e. pairings that would produce

TABLE 7.3. Data on levels of survival for offspring of okapi at different levels of inbreeding (F).

F	Lived	Died
0	86 (61%)	55 (39%)
0.125	5 (71%)	2 (29%)
0.25	12 (40%)	18 (60%)
0.375	1 (17%)	5 (83%)

Source: Based on data published in Biological Conservation 54. De Bois et al. (1990). Copyright Elsevier 1990. Used with permission of Elsevier.

offspring with a low or zero inbreeding coefficient) are then selected to breed. For example, if you, as a population manager, had pedigree data from the okapi studbook for the population under your care, like that displayed in Table 7.2, you could create pairs with little or no individual kinship to produce offspring with low inbreeding coefficients. But is this the best strategy available?

7.3.5.2. Mean Kinship Breeding Strategies

A strategy to avoid inbreeding commendably eliminates or reduces the deleterious effects of inbreeding depression in a population, but geneticists have discovered that this strategy is still not the best approach for maintaining genetic diversity (Ballou and Lacy 1995). A still more effective strategy is to select matings between captive animals that minimize population mean kinship (MK), rather than just minimizing individual kinship. Ballou and Lacy (1995) verified the efficacy of this strategy by comparing the outcomes of a variety of mating designs through computer simulation. They found that a strategy of minimizing population mean kinship was best for maximizing the retention of genetic variation. Today the ***mean kinship (MK) strategy*** is the strategy of choice in managed captive populations. In an MK strategy, individuals are paired based not only on their relationships to one another, but also to the population as a whole.

Just as most indices of diversity, such as the Shannon Index (Chapter 4) increase in value not only in response to the *number* of species present but also in response to an increasing *frequency* of rare species, so part of the success of the mean kinship breeding strategy rests on the premise that gene diversity is a measure not only of the number of different alleles in the captive population (which is a function of the gene diversity of the founders and cannot thereafter be altered) but also a measure of the frequency of those different alleles (Table 7.4), a variable which managers can manipulate through managed mating pair selections. But let us work this out further.

Recall once again the inverse relationship between mean kinship and gene diversity we examined earlier in this section,

$$1 - MK = GD.$$

As this equation demonstrates, if population mean kinship is minimized, gene diversity is maximized. Minimizing population mean kinship (in other words, lowering the average mean kinship of the population) can be accomplished by breeding individuals with low mean kinship values because these animals are the least related to others in the population. Conversely, preventing the matings of individuals with high mean kinship values has the same effect. Remember that an animal's mean kinship value (*mk*) reflects its average relatedness to all individuals in the captive population. An animal with a high mean kinship value is related to many individuals and thus carries many common alleles. But an animal with a low mean kinship value has few relatives in the population and carries fewer common alleles. Therefore, when choosing individuals for a breeding pair, it is also important to *match* the mean kinships of the individuals. Consider what happens when a breeding pair is *mismatched* in their kinship. When a pairing is composed of individuals with disparate mean kinships (low and high), the offspring will carry rare alleles from the low-MK parent and common alleles from the high-MK parent. In the future, when that offspring matures and is itself chosen for breeding, its offspring will carry both rare and common alleles. As a result, the rare and common alleles are perpetuated in equal frequency and representation is never equalized. On the other hand, by breeding animals with low mean kinship, managers can *increase* the proportion of rare alleles in the captive population, and raise the overall level of its gene diversity.

Thus, an animal's mean kinship value can serve as an index of its genetic value within the breeding program and can be used to prioritize breedings for the purpose of maintaining gene diversity. Assuming that the founding animals of a captive population are a representative sample of the wild population, an appropriate goal of captive-population managers is to preserve the genetic diversity present in the founders. Managers minimize changes from the starting gene pool by equalizing founder contributions to future generations. Individuals with low mean kinships represent founder lineages that are under-represented in the general population. If these low mean kinship animals are allowed to reproduce, their genetic contribution to the population will be increased in the next generation. Likewise, by preventing over-represented animals from reproducing, the contribution of their common alleles can be decreased. By using mean kinship to equalize the contribution of the various founder lineages in the population, managers can maintain and possibly even increase gene diversity in the next generation.

To this point we have been implicitly assuming that animals in the captive breeding group would be bred in monogamous pairs; however, many species normally breed in groups composed of a single male and multiple females (polygamy). Thus, managers of captive populations often arrange animals in groups that recreate their natural social structure. Although managing mating in social groups might at first seem more complex and problematic than managing monogamous male-female

TABLE 7.4. Two populations showing different frequencies of the same four alleles (A, B, C, D). In population 2, alleles B, C, and D are rare relative to allele A. The increased frequency of these alleles in population 1 gives population 1 a higher level of gene diversity.

Population 1	25A	25B	25C	25D
Population 2	97A	1B	1C	1D

Source: Based on data from S. Long, Association of Zoos and Aquariums. Format design by M. J. Bigelow.

pairings, social groups also can be managed to maintain gene diversity using the same criteria employed in the strategies previously discussed. For example, consider how one might employ such a strategy in a polygamous mating system, where a single male would normally mate with multiple females. First a manager would first choose a subset of males, for example, four males, from the population with the lowest mean kinship values. The manager might then choose three females for each male which also possessed low kinship values, creating a total of 12 breeding pairs. Even though offspring within groups would be more related to one another than offspring from different groups (because within group offspring all have the same father), overall mean kinship in the population remains low and genetic diversity can be conserved. Such a strategy may be necessary in captive populations with unequal sex ratios, and has the advantage of being able to increase captive population size more quickly than monogamous matings. When using a group-mating strategy, breeders normally move some individuals to different groups on a regular basis, and this practice increases the avoidance of inbreeding.

7.3.6. Making Sound Judgments in Captive Breeding Strategies: An Overview

Developing a comprehensive captive breeding strategy requires insight as well as expertise. Conservation biologists must first consider the population's source; that is, its natural history with respect to breeding patterns and social breeding groups, and whether these conditions of its natural history can be maintained and managed in a captive environment. They also must consider where the population is going. Are its offspring destined for return to natural habitats, or will they remain indefinitely in a captive environment? These and other questions must guide careful and considered decisions in the management of captive populations.

In some species, such as the black-footed ferret (*Mustela nigripes*) and California condor (*Gymnogyps californianus*), all members of wild populations are derived from individuals bred in captivity. Thus, it is not an exaggeration to say that the choices conservation biologists make as managers of such populations can be matters of life and death, not merely for individuals, but for entire species. Today's conservation biologists are aided by impressive tools for computer simulation, as well as by genetic and breeding technologies that can increase breeding success. But such technologies can never replace professional insight. When technical skill is wedded to correct purpose and attentive care, the results may be a truly worthy effort of both conservation and restoration.

Although genetic goals have become a normal part of management for captive populations, there are still few populations in the wild whose management intentionally includes genetic considerations. In the next section of this chapter, we will explore how genetic considerations might be or are being used in conservation management, and study examples of how they are actually being used to further conservation goals.

7.4. The Problem of Application: How Do We Use Genetic Information and Techniques in Conservation?

7.4.1. General Considerations

The applications of genetic techniques to conservation are varied, but can be grouped into six broad categories: (1) clarification of relatedness, taxonomy, and phylogeny among populations; (2) determination of population management units based on genetic criteria; (3) estimation of rates of gene flow and dispersal among populations; (4) determination of the time since past genetic bottlenecks in a population or the time since significant differentiation between populations; (5) understanding patterns of reproductive ecology; and (6) locating original sources of wildlife products, an important issue in the enforcement of laws protecting wildlife from commercial exploitation.

7.4.2. Genetics Can Clarify Relatedness, Taxonomy, and Phylogeny

The clarification of relatedness and taxonomy has implications for one of the most basic questions in conservation biology: how many species are there? Thus, taxonomic assessment is one of the most important applications of conservation genetics. Until the 1970s, the science of taxonomy generated little notice outside academia. Species, subspecies, and other taxonomic units were determined using the morphological characteristics of living or preserved specimens, often from very small samples. Systematic and taxonomic uncertainties were large, but of little interest or relevance outside professional circles. In the United States, all this changed with the passage of the Endangered Species Act (ESA) of 1973. The act extended legal protection to species and subspecies, making taxonomic determination a matter of life and death, as well as the basis of legal protection and the criterion for legal challenge. Geneticist Stephen J. O'Brien, reflecting on the "innocence" of taxonomic science in the years before the US ESA, wrote, "When taxonomic distinctions became the basis for legal protection afforded by the Endangered Species Act of 1973, this innocence was lost forever. Disagreements over taxonomic status fueled legal assaults on the Act, and misclassification led to inappropriate conservation measures resulting in losses of some species"

(O'Brien et al. 1996). The rise of taxonomy as a legal basis for conservation meant that taxonomic status must be established with clarity, or endangered species might be denied protection under law. Alternatively, if the determination of taxonomic status was in error, effort might be wasted on abundant species that do not need protection. If genetic information is not available for taxonomic assessment, or if has been done incorrectly so as to generate unreliable information, a host of negative consequences can result. Some endangered species might not be recognized (because they are morphologically similar to common species) and allowed to become extinct. In a captive population, separate species that are mistakenly identified as the same species might hybridize, resulting in lost genetic distinctiveness and reduced reproductive fitness. Incorrect identification could result in time, money, and effort being wasted on abundant species or hybrids misidentified as rare species. Most significantly, endangered species might be denied legal protection. Until recently, under the terms of the US Endangered Species Act, protection could only be given to a distinct species, subspecies, or population segment. This condition has been interpreted by the courts and US agencies to mean that the protected group must have unique mitochondrial DNA sequences not shared with other such groups, and that there should be differences in allelic frequencies in nuclear DNA loci, or evidence of genetically determined morphological, behavioral, or life history difference (Frankham et al. 2002:15). But without proper genetic assessment, none of these questions can be answered. Thus, genetic information can resolve taxonomic uncertainties and can also define appropriate management units for conservation (Frankham et al. 2002:365). And because the US Endangered Species Act has become the model for endangered species legislation in many countries, these genetic issues have significance to conservation efforts and protection of endangered species throughout the world.

An example of this application can be seen in the previously cited (Chapter 6) study of the Colorado chipmunk of the southwestern United States (Figure 7.11). Here Sullivan (1996) used genetic information from different chipmunk populations to identify and describe a new subspecies, *T. q. oscuraensis*, that occurs only in the Oscura Mountains of New Mexico. The new subspecies used habitats that were drier, steeper, and less vegetated than other populations, and its adaptability to these more extreme conditions permitted an expansion of overall species range (Sullivan 1996).

Similarly, recent molecular genetic studies among sea turtles differentiated the Kemp's ridley turtle (*Lepidochelys kempi*) from the similar olive ridley turtle (*L. olivacea*), vindicating the claim that the Kemp's ridley deserved recognition as a separate species (Avise 1998). Studies of the genetics of minke whales (*Balaenoptera acutorostrata*) have led investigators to advocate that the northern and southern hemisphere populations be treated as distinct species (Hoelzel and Dover 1991a). The same is true for sympatric populations of killer whales (*Orcinus orca*) (Hoelzel and Dover 1991b; Hoelzel et al. 1998). The case of killer whales is particularly interesting, as it suggests that observed differences in behavior in sympatric populations, so called "resource polymorphisms," may be genetically based (Hoelzel 1998). To give another example, Smith et al. (1991), using PCR amplification, described a new species of African shrike, colorfully known as the Bulo Burti Boubou (*Laniarius liberatus*), from a single specimen. DNA from one individual was amplified, compared to homologous sequences from other known species, and the new individual was determined to be as genetically distinct from the other species as those species were from one another.

FIGURE 7.11. The Colorado chipmunk *(Tamias quadrivittatus*), a species native to the southwestern United States in which recent genetic analysis has led to the discovery of a new subspecies (*T. q. oscuraensis*) that uses, higher, steeper, and drier habitats than other populations. (Photo courtesy of Colorado (USA) Division of Wildlife.)

Proper identification of relatedness can prevent the hybridization, and sometimes genetic extinction, of "look-alike" species in zoos and collections. For example, captive breeding of different species of gazelles and dik-diks that were mistakenly believed to be the same species has sometimes produced infertile offspring. Subsequent cytogenetic study and analysis revealed that the parents were genetically distinct and, effectively, different species (Benirschke and Kumamoto 1991). Such interbreeding of genetically different individuals and populations has further implications when individuals are transferred from one collection to another. Commenting specifically on the problem in dik-diks, Benirschke and Kumamoto (1991) note that "not only were animals of supposedly identical species chromosomally different, but also hybrids between Kirk's and Guenther's dik-diks were found in 300 collections." The authors conclude that "a cytogenetic analysis should be mandatory before captive populations are established" because "Without such planned investigations one can confidently predict that unneccesary hybridization and reduced fertility will take place in captive groups. It is similarly important that of those animals that are to be released again into nature, only cytogenetically similar animals be used" (Benirschke and Kumamoto 1991).

7.4.3. Genetics Can Define Management Units of Fragmented or Widespread Populations

One of the fundamental questions of conservation biology is: on what basis do we identify and delimit meaningful management units of populations, especially populations of conservation priority, in such a way that our management plans are sensitive and appropriate to real differences in population subunits? Because a variety of genetic techniques now permit us to more precisely determine the genetic substructure of populations, we can use genetic differences, when significant, as an objective and meaningful criterion for defining population management units.

The nation of India harbors over half of the world's population of the endangered Asian elephant (*Elephas maximus*), but, within India, populations are fragmented and widely separated. By analyzing mitochondrial DNA control region sequences as well as six nuclear DNA microsatellite markers, conservation scientist T. N. C. Vidya and her colleagues examined the genetic structure of elephants from throughout the country, and identified four demographically autonomous population units, a north-northeastern India unit, a central India unit, and two genetically distinct units in southern India that should be managed separately based on their genetic uniqueness (Vidya et al. 2005). The genetically identified units were quite different from management units proposed by the India government, which were influenced by political as well as scientific considerations.

FIGURE 7.12. The marbled murrelet (*Brachyramphus marmoratus*) of the Pacific coast of Canada and the United States, a threatened bird species which forages in offshore waters but nests in large trees in old growth forests. Genetic analysis of mitochondrial DNA in murrelets has enabled conservation biologists to identify separate and genetically distinct population segments that can serve as the basis of population management units and aid in the development of unit-specific recovery plans. (Photo courtesy of US Fish and Wildlife Service.)

Genetic techniques were used in a similar way in a recent effort to define appropriate population units for management in the marbled murrelet (*Brachyramphus marmoratus*) (Figure 7.12), a seabird of the US and Canada that forages in offshore ocean waters but nests in large trees in coastal old growth forests from central California to the Aleutian Islands. Marbled murrelets face a variety of threats in both foraging and nesting habitats, being vulnerable to deforestation and forest fragmentation, oil spills, and gill netting. Not surprisingly, murrelet populations are declining throughout their range, and they are officially listed as threatened species by both Canada and the US. Victoria Friesen and her colleagues examined the sequence variations in 547 base pair fragments from control regions of murrelet mtDNA sampled throughout its range. They found that genetics of murrelet populations were highly structured, with large genetic differences between population segments. These differences were best explained by treating populations from the western Aleutians, the central Aleutians, mainland Alaska and British Columbia, northern California, and central California as five distinct genetic management units. The authors asserted that "These populations are probably demographically independent and non-exchangeable [and] … peripheral populations may be especially vulnerable to extinction, generally small size, and often marginal habitat" (Friesen et al. 2005:612).

These and many other such studies reveal that genetic analysis can be a powerful tool in population management, providing conservation managers with increasingly sensitive analyses that can be used to identify distinct population subunits, and manage them according to special needs and circumstances.

POINTS OF ENGAGEMENT – QUESTION 2

What kinds of insights might a conservation manager derive, and what kinds of differences might it make in management strategies, if different populations of the same species, historically managed with a single strategy, were found to have highly structured (i.e. "different") genetic characteristics?

7.4.4. Genetic Techniques Can Determine Rates of Gene Flow Among Populations

Determining rates of gene flow among populations has been an important component in evaluating conservation strategies for many species. Managing gene flow among populations can help conservation biologists resolve questions of which animals to translocate to new sites, how often to do so, and when to begin and end such translocations (Frankham et al. 2002:407). For example, in Rocky Mountain bighorn sheep, Lukart and Allendorf (1996) used mtDNA to infer rates of gene flow and genetic differentiation in populations in the western United States, and found a wide distribution of mtDNA groups (***haplotypes***) over a large geographic region, suggesting that, in the past, gene flow among populations was high. However, many populations of bighorn sheep are now highly differentiated, and some have become genetically fixed for a single haplotype, suggesting more recent isolation and fragmentation of individual populations, a trend consistent with the results of Epps et al.'s (2004) study of the effect of climate change on these populations and the increasing fragmentation that would result as more and more populations at lower, warmer, and drier elevations disappear under current conditions of global warming (Chapter 5).

Measurement of gene flow is also an important consideration in plant conservation, for it is often low in small populations of rare and endemic plants. Although some studies have been able to measure gene flow directly by detecting and measuring amounts of immigrant pollen and seed, this is a difficult, labor intensive approach that simply is not feasible in many situations. Increasingly, conservation biologists have been able to assess gene flow indirectly, but accurately, by examining the distribution of genetic variation among populations (Hamrick and Nason 2000). For example, Dolan et al. (1999) used gel electrophoresis techniques to measure isozyme variation in three species of rare perennial shrubs in Florida scrub vegetation. The level of interpopulation gene flow was estimated by calculating differences among populations, as described in Chapter 6 (Wright 1951). Although levels of gene flow were different in each species, one species, *Hypericum cumulicola*, was found to be experiencing almost no gene flow among populations. This species had the lowest proportion of species- and population-level polymorphic loci, the fewest number of alleles per polymorphic locus, and the lowest level of heterozygosity (Table 7.5; Dolan et al. 1999). In a population with these characteristics and little or no gene flow, conservationists must protect many individual populations, not just a few in designated reserves, if they intend to preserve genetic diversity in the species. And because genetic diversity in this species is primarily found *among* populations rather than *within* populations, even small populations are worth preserving (Dolan et al. 1999), just as Hamrick and Nason (1996) predicted earlier in their analysis of gene flow models, genetic population structure, and their relationship to habitat fragmentation (Chapter 6).

7.4.5. Genetic Techniques Can Estimate the Time Since Past Population Bottlenecks

Inferring the length of time since past population bottlenecks is based on two characteristics of mtDNA. First, the relatively clock-like and monophyletic accumulation

TABLE 7.5. Comparison of genetic (isozyme) variation in three species of endemic shrubs of Lake Wales Ridge, Florida (USA).

	Eryngium cuneifolium	*Hypericum cumulicola*	*Liatris ohlingerae*	Endemics[a]
No. extant pops.[b]	20	90	115	–
No. of pops surveyed	16	34	30	–
No. of loci	21	18	12	
Mean no. plants/locus	30.0	28.1	22.0	–
Species-level % loci polymorphic	43.8	28.0	50.0	43.8
Population-level[c] % loci polymorphic	16.0 (1.6)	6.2 (0.9)	31.4 (1.4)	29.2
Mean no. alleles/polymorphic locus	1.61 (0.05)	1.25 (0.03)	1.93 (0.06)	2.6
Obs. heterozygosity	0.041 (0.004)	0.006 (0.001)	0.095 (0.005)	–
Exp. heterozygosity	0.054 (0.004)	0.023 (0.003)	0.121 (0.005)	0.074
Mean Nei's genetic identity	0.954	0.937	0.987	
Estimated gene flow (*Nm*[d])	0.31	0.09	1.83	

Note: [a] Cited in Godt and Hamrick (1996).

[b] Based on databases of the Florida Natural Areas Inventory and field surveys.

[c] Averaged across all populations.

[d] Calculated as $Nm = \{(1/F_{ST}) - 1\}/4$, from Wright (1951) (assumes equilibrium conditions)

Source: Dolan et al. (1999). Conservation implications of genetic variation in three rare species endemic to Florida rosemary scrub. Copyright 1999 by American Journal of Botany, Reprinted by permission of the American Journal of Botany on behalf of The Botanical Society of America.

of genetic change in mitochondrial DNA is observed in most organisms, although at different, taxon-specific rates. Second, a bottleneck renders mtDNA loci monomorphic at the time of the bottleneck. Thus, by knowing the rate of accumulated genetic change and the present level of genetic variation at mtDNA loci, one can estimate how much time has been needed to reach present levels of variation starting from a monomorphic condition.

This kind of analysis has been used on populations of Stellar sea lions (*Eumetopias jubatus*) (Bickham et al. 1996). In this case, investigators found no evidence of a recent bottleneck in the species, despite the fact that the northern population was at one time considered nearly extinct. Failure to find evidence of a genetic bottleneck suggests that large numbers of individuals survived undetected during population lows, that the lows were of such short duration that genetic diversity was not lost, or that mtDNA analysis alone is inconclusive and potentially misleading in determining historic occurrences of genetic events in populations. As noted earlier, precisely because mtDNA evolves at a different rate than nuclear DNA, conservation strategies should not be based solely on mtDNA analysis (Cronin 1993; Lukart and Allendorf 1996).

7.4.6. Genetic Techniques Can Determine Patterns of Reproductive Ecology

Using genetic analysis to understand reproductive ecology can have profound implications for conservation. For example, conservationists had long been curious about, as well as frustrated by, the question of whether adult female sea turtles returned to or near their natal areas to breed. Field observations and tagging experiments were not conclusive, but analysis of mtDNA of green turtles, loggerheads (*Caretta caretta*), and hawksbills (*Eretmochelys imbricata*) has shown that individuals in particular rookeries have fixed genetic differences in the frequencies of matriline lineages (patterns of female descent). This finding supports the hypothesis that adult females do return to their natal areas for breeding (Avise 1998). Because female sea turtles govern the reproductive output of a rookery, this discovery is significant, particularly for choosing areas to designate for sea turtle breeding refuges. It means that adult female sea turtles would be expected to breed in or near their natal areas, but not other accessible habitats, including protected areas, even if they were physically and ecologically equivalent. Thus, if the natal breeding area itself were not protected, reproductive success would then diminish or be eliminated altogether, and the loss of reproductive output in one rookery would not likely be compensated by reproduction in others.

7.4.7. Genetic Forensics: Genetic Techniques Can Determine if Conservation Laws and Treaties are Being Obeyed

Molecular genetic methods provide powerful tools for the identification of species and populations of wildlife products, including products available in retail markets, which are often the end-points for both legal and illegal exploitation of wildlife. Using PCR techniques, even small amounts of DNA, recovered from almost any biological source, can serve as a reliable identifier, even if the material has been previously cooked, canned, or processed in any variety of ways. For example, variation of mtDNA in elephants has been used to determine the sources of ivory from populations in different African countries (Bischof 1992). Although there is a ban on the sale of commercial ivory, it is likely that the ban will be lifted in the foreseeable future and that international law will allow some harvest of elephants in areas with large or destructive populations. Recall that mtDNA is inherited maternally as a linked set of genes (Cronin 1993). Because elephants have a matriarchal social system, females remain in stable family groups and several generations of related females may be present in the same group. Thus, unique mtDNA signatures may characterize populations, and even individual groups within them, and enable law enforcement officers to determine whether ivory sold on international markets has come from legal or illegal sources (Bischof 1992).

In the United States, one agency, the US Fish and Wildlife Service, has devoted an entire laboratory solely to wildlife forensics. At the National Forensic Fish and Wildlife Laboratory (NFFWL) in Ashland, Oregon, scientists use a battery of molecular genetic analyses and other techniques to analyze tissue samples from bones, hair, blood, teeth, claws, and other available body parts, as well as medicinal or food products derived from the animal, to determine their place of origin. They also use older, non-genetic forensic techniques, like examination and analysis of projectiles (bullets, arrows, spears) or other agents that may have killed the animal. Working much like a crime scene investigation (CSI) lab, the criminal cases the scientists attempt to crack are every bit as compelling as a television drama, the main difference being that, in this case, the victim was an animal, often a protected species that was illegally killed or smuggled onto international markets in violation of US or international laws. Whether the CSI is national or international in scope, the NFFWL, like a traditional police crime scene unit, attempts to use physical evidence, usually animal parts or derived products, to link a human agent (the criminal) to a particular conservation violation.

Many kinds of conservation crimes can be detected by genetic scientists at the NFFWL and other laboratories like them in other parts of the world, as well as by independent conservation scientists. To see just how powerful genetic techniques can be in identifying conservation violations and their implications, we examine the long-running investigation of the origin of "whale" products sold in Japan and Korea.

7.4.8. An Exemplary Case History: Exposing Exploitation of Protected Stocks and Species Through Genetic Forensics

Following many decades of over-exploitation and mismanagement of whaling stocks of all species worldwide, the International Whaling Commission (IWC) voted, in 1982, to impose a moratorium on all commercial whaling. Taking effect in 1986, most whale species were completely protected from commercial exploitation. Two exceptions were the northern Pacific and Antarctic minke whales (*Balaenoptera acutorostrata* and *B. bonaerensis*, respectively), relatively small (25–30 foot) baleen whales whose populations were somewhat less depleted than larger species because they had traditionally been considered too small for profitable catch per effort return. Japan is one member-nation of the IWC that has been permitted a small annual take of minke whales for "scientific" purposes. The nation of South Korea also reports "incidental" take of minke whales in their commercial fishing operations. Both of these sources of minke whales are legal under international law, and the whale products can be sold in commercial markets in both countries. To test whether the "whale" products in these countries were derived from these legal sources, C. S. Baker of the University of Auckland (New Zealand) and his colleagues purchased products labeled as "whale" meat from retail outlets from 1993 through 1999. Using a phylogenic analysis of base sequences from the mtDNA control region that could be compared to existing data on various cetacean species, Baker et al. determined that the whale products included tissues and organs from eight species or subspecies of baleen whales (including the two species of minke whales), two species of sperm whales, two species of beaked whales, porpoises, killer whales, numerous species of dolphins, and sheep and horses. Although genetic analysis revealed that the majority of the "whale" products (68%) in these markets were indeed from minke whales, the other six baleen species and the sperm whales represented in the markets were protected by international law and most had not been hunted legally for many years. Further analysis revealed that the proportion of minke whale products present could not have been generated from scientific and incidental take alone, and that much of this product did not come from the southern (Antarctic) stock of minke whales, but originated from the so-called "J" stock, a depleted population living in the northern Pacific, including the Sea of Japan, that is now, by international law, a protected population. Taking the analysis further, Baker et al. examined genetic identifiers from minke whales known to have been taken for scientific research and compared them to minke whale products sold in commercial markets. Disturbingly, the market sample was significantly different in genetic characteristics from the scientific catch, indicating that most of these products did not come from scientific hunting, but from undocumented (i.e. illegal) exploitation of the supposedly protected J stock (Baker et al. 2000).

Using their knowledge of the market proportion of minke whale products and the known scientific catch (from a different stock of minke whales) Baker et al. were able to estimate that approximately 100–150 minke whales were being taken each year from the J stock to supply the observed proportions of it in Japanese and Korean markets. Insightfully taking their analysis to its final step, Baker et al. used their data to model expected future trends in the J stock of minke whales based on this level of annual take. Their model (Figure 7.13) indicated that, at these take levels, the "protected" J stock of minke whales would continue to decline (Baker et al. 2000).

Three important questions were answered in this investigation. First, were whale products sold in legal commercial markets derived from legal scientific take? No, many whale products represented unreported exploitation of endangered whale species, as well as products not from whales at all. Second, were the products from scientific

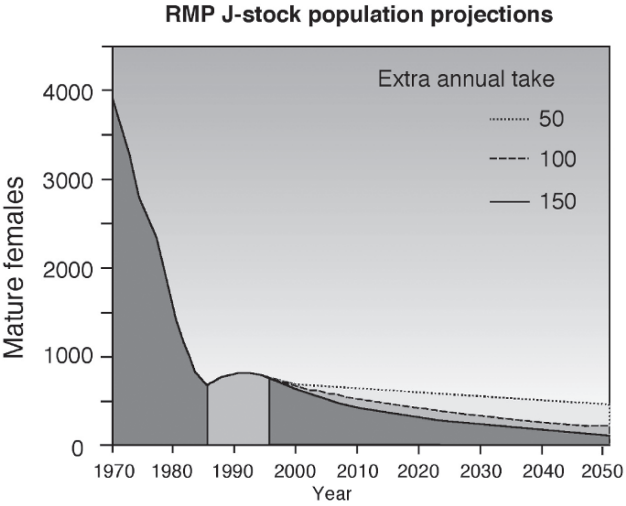


FIGURE 7.13. Estimated history and predicted future decline of the J-stock (northern Pacific/Sea of Japan) of minke whales (*Balaenoptera acutorostrata*) under three assumed levels of incidental take (50, 100, and 150 whales per year) from 1998 onward. Incidental take levels represent estimated take needed to account for past frequency of minke whale products in Japanese and Korean markets (100–150 whales per year) and a conservative, lower estimate (50 whales per year) in case of overestimation or more effective enforcement of protective statutes. Note that, regardless of level of incidental take, the J stock continues a steady decline through 2050. (Baker et al. 2000. Predicted decline of protected whales based on molecular genetic monitoring of Japanese and Korean markets, Figure 3. Proceedings of the Royal Society of London. Copyright 2000 Royal Society of London. Reproduced with permission of the Royal Society of London and C. S. Baker.)

take (minke whales) from abundant (Antarctic) stocks? No, six times as much of the minke whale products were from the protected J stock as from the Antarctic stock. Finally, what proportion of undocumented whale products in these markets came from "protected" species and populations? Sadly, approximately 10% of the products came from protected species and 31% from protected stocks of minke whales (Baker et al. 2000).

Discouraging as these findings are, their publication in this and related studies exposed illegal activity and have contributed to increased international efforts to stop illegal exploitation of protected stocks and species, not to mention consumer fraud. Such exposure provides the basis for more vigorous enforcement by wildlife enforcement agencies, as well as incentive for heightened awareness among consumers who do not want to be party to the illegal exploitation of endangered animals.

7.5. Building Genetic Insights into Conservation Management

7.5.1. Advanced Technologies, Limited Applications: The Current State of Genetic Considerations in Field Conservation

The phenomenal advances in genetic technology and assessment during the past 20 years have given conservation genetics an increasing role in the management of captive populations, conservation forensics, taxonomic clarification, and conservation law. Despite these advances, genetic considerations still often play relatively little part in actual management of *in situ* populations. But they should, because we now know, from an increasing number of studies, that the loss of individuals in a population, even in common species, often results in a loss of genetic diversity in that population. One of the clearest examples of such loss comes to us from a study of logging in tropical forests. In these forests, forest geneticists Wickneswari Ratnam of the Universiti Kebangsaan (Malaysia) and Timothy Boyle of the United Nations Development Programme determined that logging that reduced the average basal area of trees by 56% also reduced expected heterozygosity and genetic diversity (Shannon Index) by 5–23.4% in five different species, each with a different life history strategy, and the loss of alleles for different species ranged from 7.7% to 25.0%. Similarly, logging of white pine (*Pinus strobus*) that removed 75% of trees in a temperate forest in Canada resulted in a loss of more than 30% of all alleles, and an 80% loss of rare alleles (Ratnam and Boyle 2000).

Despite these and many other examples from field studies, genetic considerations still are not primary concerns in most *in situ* population management strategies. The best available models for population growth and viability analysis, such as VORTEX, ZooRisk, and GAPPS, are increasingly incorporating capacities for genetic management of populations, and many modelers are now building custom models for managers of specific populations that incorporate a full range of genetic effects, but, in the field, onsite management of populations still tends to underestimate and under-incorporate genetic considerations. Creating a larger role for genetic considerations in the actual management of wild populations will require conservation biologists to:

1. Intentionally build genetic considerations into long-term management strategies
2. Extrapolate appropriate strategies for most taxa from relatively few studies of model species, at least for the foreseeable future
3. Identify more precisely under what circumstances genetic considerations could limit the size or distribution of managed species
4. Use genetic data more often, more systematically, and more intentionally to better understand population and extinction processes

Although it remains rare for ongoing *in situ* management plans in conservation to consider genetic objectives as primary concerns, some conservation efforts are beginning to try. One such initiative is the development of the Genetic Conservation Reserve.

7.5.2. Genetic Conservation Reserves: Genetics as a Basis for Reserve Design

Traditionally, nature reserves have been established to protect particular species of interest, to preserve ecosystems and their processes and functions, or to preserve representation species biodiversity at landscape levels (Chapter 1). However, there is no logical reason why reserves could not be established for the purpose of preserving genetic diversity, especially in areas where genetic diversity of populations may be disproportionately high. The "hotspot" approach to biodiversity conservation (Chapter 4) implicitly assumes protection of genetic diversity, although its actual conservation targets are species. Recently, some conservation agencies and organizations have begun to make genetic diversity or, in some cases, genetic uniqueness, more explicit as a criterion in reserve selection by establishing ***Gene Conservation Reserves*** (GCRs) or ***Gene Resource Management Units*** (GRMUs). For example, the Washington (US) Department of Natural Resources has set aside over 100 areas to preserve particular genotypes of an ecologically and economically important conifer, the Douglas fir (*Pseudotsuga menziesii*). Individual reserves are small, averaging about 10 ha in size, but each reserve usually contains more than 400 large individuals of this species.

In developing GCRs, geneticists James Hamrick and John Nason draw on insights gained from their previously discussed studies of the effects of life history and pollination-dispersal strategies of plants. Using simple probability theory, they note, in the cases of some individual plant species and populations, that, because the proportion of genetic diversity within and among populations can vary widely, conservation strategies should consider the dispersal ability of the targeted species. For example, Hamrick and Nason state that "… since 90 percent of the genetic variation in wind-pollinated species resides within their populations, more than 99 percent of the total genetic diversity of the species can be maintained with three strategically selected reserves.… In comparison, for a selfing population with only 50 percent of its total genetic diversity occurring within an average population, approximately ten populations would need to be preserved to insure that 99 percent of its genetic diversity is maintained" (Hamrick and Nason 1996:227).

Some genetic conservation reserves already exist, and some, more traditionally established reserves are trying to effectively serve this purpose, especially with regard to threatened plants. A critical question of a GCR is "Does it work? Is genetic diversity actually conserved?" In plant conservation, the question can be taken one step further. Do we really need *in situ* nature preserves to conserve plant genetic diversity, or could we accomplish the same thing with less effort and expense in new or existing *ex situ* plant collections and botanical conservatories? Conservation geneticists Qiaoming Li and his colleagues at China's Xishuangbanna Tropical Botanical Garden addressed this question directly, and ingeniously, by comparing the amount of genetic diversity of an endangered tree, the Chinese parashorea (*Parashorea chinensis*), that was present in seven natural populations, including three in Chinese nature preserves, with that of an *ex situ* population conserved in the Xishuangbanna Tropical Botanical Garden. Their analysis used nearly the full range of genetic technologies that we have discussed previously. Starting with genomic DNA amplified via PCR techniques and fragmented using RAPD, Li and his colleagues then employed eletrophoresis to separate the RAPD markers into identifiable bands. The amplified products of the RADP, as bands, were scored discretely as present (1) or absent (0). From banding data, Li et al. then were able to estimate the level of genetic diversity in each population.

The Botanical Garden population (*ex situ*) contained 77.1% of the total genetic variation of *P. chinensis* and 91% of moderate to high frequency RAPD fragments (fragments with frequencies greater than or equal to 0.05). In contrast, populations in the three *in situ* nature preserves possessed 81.4% of available genetic variation and 95.7% of moderate to high density fragments. Thus, Li et al. concluded that the *ex situ* trees lacked sufficient genetic variation to meet the needs for future releases of *P. chinensis* to the wild, but populations in nature reserves did contain sufficient genetic variation to maintain long-term survival and evolutionary potential of this species (Li et al. 2005).

7.6. Synthesis

Genetic techniques in conservation have made possible non-invasive and less labor-intensive sampling of wild populations, vastly enhancing the potential of genetic management. In the realm of captive breeding, the accelerating pace of development in genetic analysis has elevated this field from being the art of a few specialists to a science that can be practiced with an increasingly uniform set of standards and protocols. Further, improved genetic techniques and analysis have changed captive breeding from an effort that once seemed a last desperate gamble for species salvation into carefully coordinated programs with real potential for successful long-term species preservation and re-introduction of animals and plants to natural areas.

The danger inherent in a period of such achievement and optimism in conservation genetics is that, improperly applied and incorrectly understood, genetic analyses can lead to inappropriate conclusions, incorrect management decisions, and disillusionment due to overinflated expectations. An overemphasis on genetic analysis, to the exclusion of other considerations of a population's identity or persistence, can produce management recommendations that might be inappropriate, or, in extreme cases, even absurd. For example, the US Fish and Wildlife Service (1990) recovery plan for the endangered plant, Peter's mountain mallow (*Iliamna corei*), called for collection of data on genetic variation and subsequent development of a population genetics model to determine the number of populations and effective population sizes required for long term survival. Botanist Douglas Schemske and his co-workers, commenting on the plan, noted, "This emphasis on the genetics of conservation rarity is a clear case of overkill, as only four individuals of the mallow are known to exist in the wild" (Schemske et al. 1994). To avoid such "genetics conservation overkill," conservation biologists must take pains to not misappropriate genetic techniques or seek excessive amounts of genetic information when it is has little value for the immediate needs of conservation planning, and to understand the distinctive concepts and context of genetic techniques so that their results are properly understood and fully integrated with other sources of information and insight. At the same time, conservation biologists working with *in situ* populations must not continue to de-emphasize or ignore genetic considerations in developing management and recovery plans for wild populations.

As genetic considerations do, rightly, come to have a greater part in all dimensions of conservation planning, conservation biologists must understand that genetic analyses do not, in themselves, make management decisions for them. Non-genetic dimensions of a species' life history, environmental constraints, or population demography will remain important to the persistence of a species, as will an understanding of the present state of its genetic diversity. Nevertheless, although genetic analysis can never be a substitute for professional judgment and insight, it must increasingly be an intentional aid to it, so that environmental adaptability and genetic potential are preserved in every species, not merely remnant, and genetically impoverished populations that will have little hope of long term persistence.

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8

The Conservation of Populations: Concept, Theory, and Analysis

> *I have seen something else under the sun: the race is not to the swift, or the battle to the strong, nor does food come to the wise, ... but time and chance overtake them all.*
>
> Ecclesiastes 9:11

In this chapter, you will learn:

1. **What populations are**
2. **What factors determine the size and persistence of populations**
3. **What causes populations to decline and become extinct**
4. **What metapopulations are and how they can be conserved**
5. **How to use population viability analysis to determine important threats to population persistence**

8.1. Defining Populations

The traditional definition of ***population*** is "all coexisting individuals of the same species living in the same area at the same time." As noted in Chapter 4, the species concept, upon which this definition depends, has been subjected to new interpretations, particularly as genetic techniques provide increasing precision on measurements of genetic similarities and differences of organisms. Wells and Richmond (1995) argue that spatial, genetic, and demographic structure define a group, and that a population is a group of individuals showing a clear disjunction from other groups in at least one of these characteristics.

Spatial disjunction refers to a distribution pattern in which groups of individuals, although physically or genetically similar, are separated from one another by location. Consequently, individuals from one group are not able to interact with individuals in other groups. To be considered disjunct, each group must occupy a particular area relative to other groups, the space between the groups must not contain individuals of any group, and individuals must not normally travel from group to group. Spatial disjunction is one criterion for defining populations, and is the easiest to detect.

G*enetic disjunctions* occur when all the individuals in one group share a common set of genetic attributes that are not shared by individuals in other groups. If two groups share two common genes, 1 and 2, but the first group contains alleles A and B at gene 1 and C and D at gene 2, while the second group contains alleles W and X at gene 1 and Y and Z at gene 2, then the groups are genetically disjunct and, hence, distinct populations.

A *demographic disjunction* occurs when a group of individuals shares common demographic properties that differ in value from the same properties in other such groups. The best conceptual explanation of this kind of disjunction is provided by Cole (1957), who defined a population as "a biological unit at the level of ecological integration where it is meaningful to speak of a birth rate, a death rate, a sex ratio, and an age structure in describing the properties of the unit." Cole's definition identifies populations as groups that have common rates of birth and death, characteristic sex ratios and age structures, and other demographic properties. To produce demographic discontinuity, different groups must experience too few exchanges of members to significantly affect one another's demography. If immigrants from one group do markedly change the birth rate, death rate, age structure, or sex ratio of another group, then the discontinuity is broken and the two groups are, from a demographic standpoint, really one.

Among these three types of discontinuities, spatial discontinuity is the most important. If the populations are not separated spatially, the other criteria will not exist. For example, if we find a variety of alleles in many individuals of the same species, but we cannot delineate in space how the alleles are segregated, then we have no genetic discontinuity, only genetic variety. And as any good conservation geneticist knows, the first step in identifying genetic differences is to look for spatial disjunctions (Wells and Richmond 1995). Although spatial discontinuity could occur without genetic or demographic discontinuity, it is difficult to imagine how genetic or demographic discontinuity could occur without spatial separation.

When we refer to a group of individuals as a "population," we must identify the discontinuity – spatial, genetic, or demographic – that exists between this group and other groups. If we find no discontinuity, then the group of individuals we are examining, however fascinating they may be, do not constitute a population. Instead they form a part of some larger population that is in some way disjunct from other groups.

Populations are the fundamental unit of conservation and the primary target of management and policy directives that provide meaningful protection to groups of organisms that are declining or small in number, or facing the imminent threat of extinction. Having defined populations, the next step is to determine what factors determine their size and persistence.

8.2. Basic Population Processes and Small Populations

8.2.1. Population Demography

Extinction, the quality of "ceasing to be," marks the termination of a population's existence. This is an event that conservation biologists seek to avoid, but few populations suddenly disappear when they are large, vigorous, and growing. In almost all cases, extinction is preceded by decline. The genetic dangers faced by small populations have been examined in Chapters 6 and 7. We now explore other factors than can cause population decline and eventual extinction.

Traditionally, population growth is defined by birth, death, immigration, and emigration. In a group of individuals born at the same time (cohort), the sum of the probabilities of survival of each individual to a particular age (survivorship) influences the trajectory of population change over time. As losses of individuals represent subtractions from the population, more individuals are added by births, a process known as ***recruitment***. Recruitment is driven by ***fecundity***, the number of young or eggs produced per female (animals) or seeds per individual (plants) per unit time. Other increases that accrue to the population through immigration, and additional losses that are incurred through emigration, are functions of ***dispersal***, the permanent movement of an organism from its area of birth to a new area. Dispersal must be measured in terms of both *rate* (proportion of individuals that leave the natal area) as well as *distance* (how far an organism travels from the natal area before it resumes a settled existence).

Simple models of population growth integrate the complexities of these multiple factors with relatively few mathematical concepts. The simplest model of all is that of ***exponential population growth***, which is defined solely by the population's size, N, and its rate of increase, r, which is defined as the difference between the population's rate of birth (b) and its rate of death (d). Immigration and

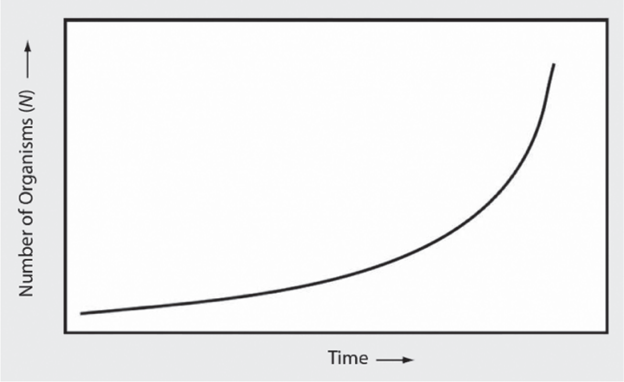

FIGURE 8.1. The exponential growth curve, a graphical depiction of a population increasing at an ever increasing rate over time. (Illustration by M. J. Bigelow.)

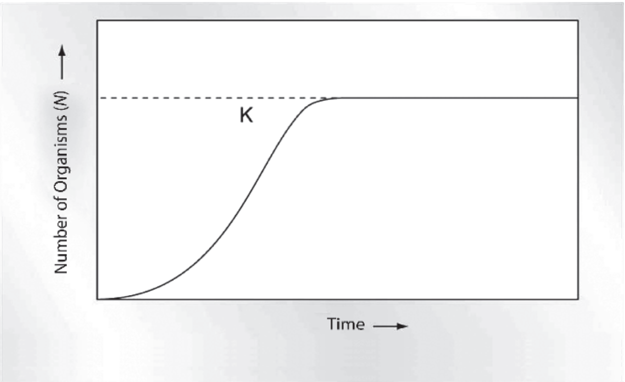

FIGURE 8.2. The logistic growth curve, a graphical depiction of a population's growth as it approaches an environmental limit or carrying capacity. (Illustration by M. J. Bigelow.)

emigration are either ignored, considered inconsequential or added to the values of *b* and *d*, respectively. In exponential growth, the change in numbers (*dN*) in the population over change in time (*dt*) is determined by the equation

$$\frac{dN}{dt} = rN.$$

Viewed graphically, exponential growth is a J-shaped curve showing a population growing over time at an ever-increasing rate (Figure 8.1).

Exponential growth is not a realistic, long-term phenomenon in any population that is influenced or affected by its environment. As biologist Mark Boyce remarked bluntly about the exponential growth model, "it has no ecology" (Boyce 1992). A real population has an ecology, and an accurate model must, at least to some degree, reflect it.

The simplest model of population growth that is affected by the environment is ***logistic growth***, which includes an environmental limit on the population size (the carrying capacity) that slows population growth as *N* approaches this limit, *K*. Logistic growth is mathematically defined as

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right).$$

When *N* is small relative to *K*, $\left(\frac{K-N}{K}\right)$ approaches unity, and the population grows at an exponential rate. But as *N* approaches *K*, the value of the expression approaches zero, and so does the rate of growth, *dN*/*dt*. Thus, a visual representation of the model depicts a population growing at a nearly exponential rate during early stages of growth, but gradually slowing until it reaches a stable equilibrium (Figure 8.2).

Many variations, some extremely sophisticated, have been developed to increase the correspondence between the logistic growth model and real populations, most of which do not move smoothly or uniformly toward equilibrium or necessarily stay there if they achieve it. The model described above assumes that (1) each new individual has an instantaneous effect on the population's growth rate, an assumption which is almost always false; (2) individuals are added to the population at a constant rate, a condition not met by many populations; and (3) carrying capacity is constant, when in reality it varies according to environmental variation and interaction with the effects of the population on available resources. It is more accurate to define carrying capacity (K) not as a constant value that a population cannot exceed, but as a population size reflecting an equilibrium between a population and its resources. Thus the value of K varies environmentally. For example, herbivore populations can lower the value of K by damaging their plant food resources in ways that reduce the plants' long-term productivity (Caughley 1979).

The logistic model also assumes that all individuals in a population are essentially demographic equivalents of one another in reproduction and survivorship. This is rarely true, especially in populations with long-lived individuals, where population growth is often defined and determined by ***age structure*** and ***sex ratio***. With sufficiently detailed information, one can construct a ***life table*** and compute age-specific rates of birth, mortality, survivorship, fecundity, and other parameters that determine the growth of a given population (Table 8.1, Appendix).

Although life tables are valuable tools for identifying the specific traits of populations that determine patterns of growth over time, they have limitations. One is the assumption that the demographic parameters in the life table remain constant over time. A second limitation is that life tables focus on a population's past, but conservation biologists are primarily interested in its future. Instead of simply asking about past or present demographic parameters of a population, a conservation biologist would ask, "What is the likelihood of this population persisting if these parameters

Table 8.1. An example of a life table for Belding's ground squirrel (*Spermophilus beldingi*). Life tables, properly constructed from appropriate data, provide important summaries of the age-specific demographic characteristics of plant and animal populations.

	Females					Males				
Age (year)	n_x	d_x	l_x	q_x	e_x	n_x	d_x	l_x	q_x	e_x
0–1	337	207	1.000	0.61	1.33	349	227	1.000	0.65	1.07
1–2	252[a]	125	0.386	0.50	1.56	248[b]	140	0.350	0.56	1.12
2–3	127	60	0.197	0.47	1.60	108	74	0.152	0.69	0.93
3–4	67	32	0.106	0.48	1.59	34	23	0.048	0.68	0.89
4–5	35	16	0.054	0.46	1.59	11	9	0.015	0.82	0.68
5–6	19	10	0.029	0.53	1.50	2	0	0.003	1.00	0.50
6–7	9	4	0.014	0.44	1.61	0	–	–	–	–
7–8	5	1	0.008	0.20	1.50	–	–	–	–	–
8–9	4	3	0.006	0.75	0.75	–	–	–	–	–
9–10	1	1	0.002	1.00	0.50	–	–	–	–	–

[a] Includes 122 females first captured as yearlings

[b] Includes 126 males first captured as yearlings

Source: Sherman and Morton (1984). Reprinted with permission of the Ecological Society of America.

remain unchanged, and for how long?" Although the questions are related, they are profoundly distinct. We now take up these questions in more detail.

8.2.2. Stochastic Perturbations

8.2.2.1. Deterministic Versus Stochastic Factors

To determine the probability that a population will persist in time, and for how long, we must evaluate the factors that affect the population's size. Such factors can be broadly categorized as deterministic or stochastic. ***Deterministic factors*** are those that affect the population in a constant relation to the population size. For example, if predators consistently removed 10% of all individuals in a population year after year, regardless of variations in the population's size, we would be justified in calling predation a deterministic factor. Rarely, however, is any factor affecting a population such a simple, cause-and-effect relationship that can be counted on to produce a determined and predictable result. Factors that significantly influence population size are almost always ***stochastic factors***.

In his classic paper, "Minimum Population Sizes for Species Conservation," US Fish and Wildlife Service biologist Mark Shaffer identified four "sources of uncertainty" that can affect the size of a population: ***genetic stochasticity***, ***demographic stochasticity***, ***environmental stochasticity***, and ***natural catastrophes*** (Shaffer 1981). All of these can be considered stochastic rather than deterministic in that their effects are not certain, but rather come from a random distribution of events whose probabilities are unique to particular populations and their environments. If a population is large, the outcomes associated with these sources of uncertainty (stochastic variation) follow the law of averages. But if the population is small, its success or failure may deviate drastically from the average because it often hinges on chance events that affect only a small number of individuals, sometimes with devastating results. For example, the heath hen (*Tympanuchus cupido cupido*), a bird similar in appearance and behavior to the North American prairie chicken, was once common throughout the northeastern US. By 1876, overhunting and habitat destruction had restricted its range to the island of Martha's Vineyard in Massachusetts (Shaffer 1981). By 1900 there were fewer than 100 survivors, and a refuge was established for the population on the island in 1907. By 1916, the population had increased to around 800 individuals and seemed to be headed for recovery. Then a series of environmental and demographic "bad luck" befell the survivors. In the year of their peak population, a fire devastated the island and destroyed most of the remaining habitat and nests. A high winter concentration of goshawks (*Accipiter gentilis*), an efficient avian predator, deepened the decline. After a minimal recovery in 1920 to 100–150 birds, disease swept through the population, eliminating all but 100 individuals. Losses continued from this point on, with increasing numbers of birds experiencing sterility. Worse, the proportion of males increased until, in the final years, there were no females at all! The population was extinct by 1932.

The factors of environmental stochasticity, demographic stochasticity, genetic stochasticity, and natural catastrophe – the "Four Horsemen of the Extinction Apocalypse" – were all active in the demise of the heath hen. Although they are complex and interactive, we will examine each factor briefly and individually.

8.2.2.2. Genetic and Environmental Stochasticity

Problems of genetic stochasticity inherent in small populations have been explored previously, but are briefly reviewed here. Small populations tend to suffer from increased rates of inbreeding, increased effects of genetic drift, and the accumulation of unfavorable mutations. Many small populations in the wild, such as the Florida panther (O'Brien et al. 1996), and captive-bred populations of endangered species have shown measurable detrimental effects associated with inbreeding depression and genetic drift. These effects accumulate in small populations and can lead to further population declines and eventual extinction.

Environmental stochasticity refers to fluctuations in the probability of birth and death due to the temporal variation of habitat parameters; populations of competing, parasitic, or predatory species; and incidence of disease. The importance of environmental stochasticity can be best understood relative to the average rate of increase of the population. Let r_{av} represent that average rate and let V_e represent the variance in population growth attributable to environmental variation. If r_{av} is greater than V_e, then the expected persistence time of a population increases directly with increasing population size at an ever-increasing rate (Figure 8.3). In this scenario, environmental stochasticity is unlikely to cause extinction as long as the population is not very small. On the other hand, if V_e is greater than r_{av}, the shape of the population persistence curve is different. Persistence time still increases as the size of the population increases, but it reaches an upper asymptote, beyond which further increases in population size do not significantly increase expected time of population persistence. This second case describes a population with large, environmentally induced population fluctuations and a relatively small rate of increase. In such a case, even large populations would be very vulnerable to extinction, and the best protection against extinction would not necessarily be to generate the largest population, but to ensure that the total population did not all experience the same environmental variations at once (Simberloff 1998).

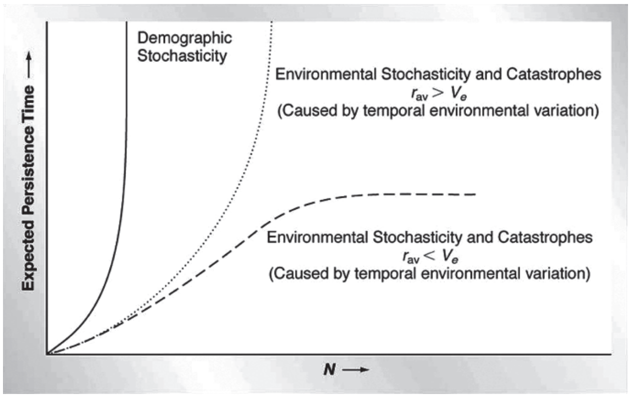

FIGURE 8.3. The effects of environmental and demographic stochasticity on the persistence time of a population. Note that while the probability of extinction from such forces is very low in large populations, these factors create a high probability of extinction at low populations. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications,* Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

8.2.2.3. *Demographic Stochasticity*

Demographic stochasticity refers to random fluctuations in birth and death rates, emigration and immigration, or sex ratio and age structure of a population. Such processes are still stochastic even if the observed rates remain constant. Biologist Robert Lacy noted that "with the exception of aging, almost all events in the life of an organism are stochastic" (Lacy 1993). In large populations, variation among individuals rarely matters; in small populations, it matters very much. Loss of a pregnant female, a new generation with a skewed sex ratio, or the accidental death of a few breeding adults can have enormous impacts on small populations. Like environmental stochasticity, the effects of demographic stochasticity diminish with increasing population size, and population persistence is all but assured (Figure 8.3). But, at small population levels, the effects of demographic stochasticity alone make extinction almost certain.

A further consideration of demographic stochasticity that weighs heavily on small populations is the so-called "***Allee effect,***" named for the British ecologist, W. C. Allee, who first described it (Allee et al. 1949). Compared with large populations, individuals in small populations may "suffer reduced fitness from insufficient cooperative interactions with conspecifics" (Lande 1999). The outcome of such "insufficient cooperative interactions" can trigger a number of different mechanisms, acting alone or in concert, that reduce the population's fitness. In populations below a certain size or density, individuals, as geneticist Russell Lande puts it, "may have difficulty encountering potential mates. These effects can render population growth negative in small populations, creating an unstable equilibrium at small population size below which the population tends to decline to extinction" (Lande 1988). There are other detrimental effects of small population size on fitness. In some populations, social groups stimulate mating activity. For example, some gallinaceous birds (Order Galliformes) like the sage grouse (Figure 8.4) and prairie chicken, gather for mating on communal display and breeding grounds known as leks. If numbers are insufficient to promote lek formation, displays and breeding may not take place. Also, in many species, groups may deter predators through cooperative defense and increased vigilance or increase foraging efficiency by altering the vegetation community itself (McNaughton 1984). When density drops below a level at which such groups can form, the ability to detect predators decreases, vegetation can no longer be altered for optimal foraging efficiency, and survivorship may decline. In other species, groups of

FIGURE 8.4. The sage grouse (*Centrocercus urophasianus*), a gallinaceous bird of the western United States, gathers for mating on communal display and breeding grounds known as leks. If numbers are insufficient to promote lek formation, displays and breeding may not take place. (Photo courtesy of US Bureau of Land Management.)

individuals may benefit one another through various means of physically or chemically conditioning the environment (such as huddling for warmth or making trails through heavy snow that can be used repeatedly to save energy), or through communal nesting (for example, weaverfinches, Family Ploceidae). At very low densities, animals may be unable to take advantage of these and other benefits they formerly enjoyed when living in larger groups. Because of the Allee effect, there may be a minimum threshold density in small populations below which the population may be unable to recover.

8.2.2.4. Natural Catastrophes

Some (for example, Simberloff 1998) have argued that natural catastrophes are simply extreme cases of environmental stochasticity. There is some sense in which this is true, as natural catastrophes often are extreme forms of normal environmental variation (e.g., extreme and prolonged drought or flash floods resulting from intense, heavy rain). But catastrophes also may be considered a separate category because they occur so infrequently as to lie outside the normal probability distribution of random events associated with environmental variation. Further, catastrophes may be qualitatively as well as quantitatively different in their effects. In the understated words of biologist Robert Lacy, “a forest fire is not just a very hot day” (Lacy 1993). Catastrophes, although rare, pose special threats for small populations because they have the potential to eliminate all individuals in a small group. The most viable protection for small populations, then, against catastrophes is spatial dispersion.

Many populations in nature are spatially dispersed whether managed or not. Yet, with such dispersion, gene flow via exchange of individuals retains connectedness between such population subunits. When a population consists of multiple, spatially separated subunits, with varying degrees of interchange of individuals, we must modify our understanding of *population* to take conditions into account. We must begin to understand the concepts, functions, and processes associated with *metapopulations*.

8.3. Populations and Metapopulations: Complexities of Population Subdivision and Fragmentation

8.3.1. Origins of Metapopulation Theory

We have already explored the genetic implications of spatially separated populations, or metapopulations (Chapter 6). Now we must examine their demography. As noted earlier, population ecologists H. G. Andrewartha and L. C. Birch stated over 50 years ago that “a natural population occupying any considerable area will be made up of a number of … local populations” (Andrewartha and Birch 1954). Accompanying their definition, Andrewartha and Birch provided a schematic illustration of a series of spatially subdivided populations of a species with different densities in each subunit. This seemingly innocuous statement and illustration initially generated little attention, but it is probably one of the first conceptual expressions of the concept of a population existing as spatially disjunct subunits at different densities in habitat patches of varying carrying capacity. Andrewartha and Birch also noted that individual subunits suffered periodic extinction, followed by recolonization by individuals dispersing from neighboring subunits. By making these traits explicit, Andrewartha and Birch functionally defined a *metapopulation*, though the word would not appear in scientific literature for many years.

The view of populations as subdivided by interacting units was made more explicit by the biologist C. B. Huffaker and his co-workers in an elegant series of experiments involving mites and oranges in the late 1950s and early 1960s (Huffaker 1958; Huffaker et al. 1963). Huffaker’s work, designed to evaluate dynamics of predator–prey relationships predicted in traditional Lotka-Volterra models, used the six-spotted mite (*Eotetranychus sexmaculatus*) as the prey species, and another species of mite (*Typhlodromus occidentalis*) as the predator. Both can sustain large populations on the skin of an orange, so Huffaker created “habitats” of oranges and “non-habitats” of rubber balls placed in various combinations on a tray. Mites could not leave the tray, but could move among the balls and oranges (Figure 8.5). When the prey species was forced to feed in habitats (oranges) concentrated in large areas and grouped at adjacent, joined positions, predators exterminated prey within 2 weeks, whereupon all predatory mites starved. When oranges were dispersed, prey survived longer, and predator and prey populations followed regular cycles of increase and decrease (Figure 8.6) (Huffaker et al. 1963).

Such experiments, and others that followed, demonstrated the importance of environmental heterogeneity in maintaining the stable predator–prey interactions predicted by the Lotka-Volterra model. They also demonstrated that populations can, under certain circumstances, persist as "subpopulations" that occupy fragmented habitats on a temporary basis, and may move regularly from one habitat subunit to another. In this case, individual subpopulations suffer extinction, and only a portion of all available habitats is occupied at any one time, yet the population persists.

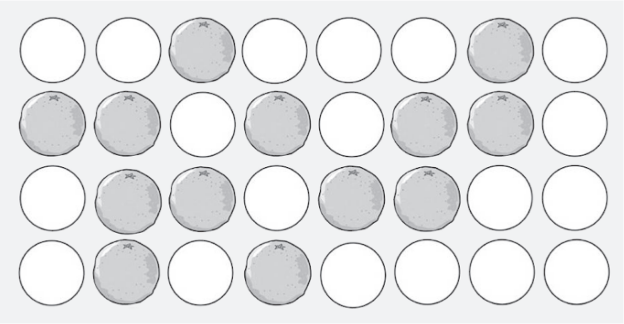

FIGURE 8.5. A diagrammatic representation of Huffaker's experiment (Huffaker 1958; Huffaker et al. 1963) on the persistence of a predator–prey system of two species of mite. Dark circles represent oranges that mites could colonize and white circles represent rubber balls that they could not colonize. (Illustration by M. J. Bigelow.)

8.3.2. The Definition and Development of Metapopulation Concepts

Huffaker created fragmented habitats in his laboratory by the random placement of oranges and rubber balls. The process of fragmenting habitats similarly divides formerly contiguous populations into spatially discrete population subunits. The concept of metapopulations was developed to describe such conditions as an alternative to the traditional view of populations as demographically homogeneous units having no group structures. This alternative emerged as an explicit model in the late 1960s and early 1970s when Levins (1970) offered the first intentional definition of a metapopulation as "any real population [that] is a population of local populations which are established by colonists, survive for a while, send out migrants, and eventually disappear" (Figure 8.7).

Levins' theory of metapopulations arose from an examination of habitat heterogeneity and problems associated with the control of insects that damaged crops. In a paper presented at the symposium "Genetics in Biological Control" at the 1968 Meeting of the Entomological Society of America, Levins stated that his purpose was "to show that the pattern of environmental variation in space and time can be utilized in the control of pests and to indicate the information which is needed for the selection of the most promising predator" (Levins 1969). Indeed, Levins' practical objective was to determine the optimum properties of the predator population that could control the pest

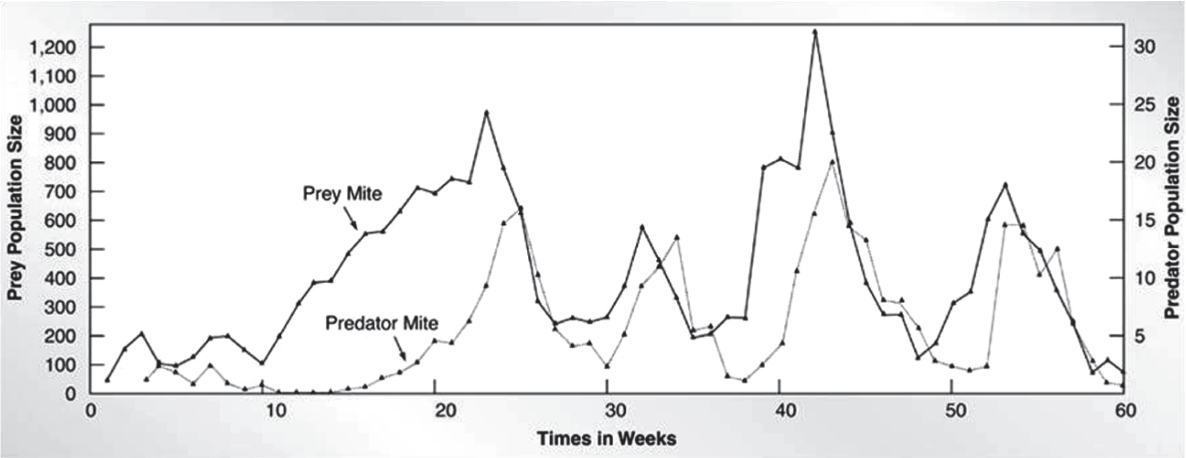

FIGURE 8.6. Oscillations in the densities of the predatory mite, *Typhlodromus occidentalis*, and its prey, the six-spotted mite, *Eotetranychus sexmaculatus*, in Huffaker's experimental system of oranges (habitat for *Eotetranychus sexmaculatus* which feeds on oranges) and rubber balls (non-habitat) over a period of 60 weeks. Note that predator and prey populations follow a series of regular synchronized fluctuations. (Courtesy of *Hilgardia* 27:343–383, p. 370. Copyright 1958 by the Regents of the University of California.)

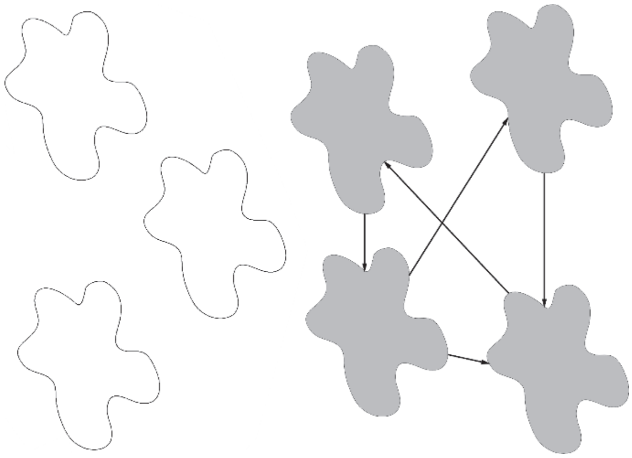

FIGURE 8.7. The Levins' Model of Metapopulations. Levins' metapopulation model portrays extinction and migration patterns of individuals living in discrete subunits. Without recolonization of the habitat, each local population is in danger of becoming extinct. Arrows represent population recolonization. Open areas represent populations that have become extinct due to the lack of immigrants. Solid areas are occupied habitats. (Based on concepts described by Harrison 1991. Illustration by M. J. Bigelow.)

and then to produce such a population through genotypic selection. His purpose was to move entomologists away from the concept of thinking about "average" conditions and concentrate instead on using specialized predators that would not be uniformly effective in all environments (Levins 1969). The concept of the metapopulation, as Levins had defined it, received little attention from conservation biologists for nearly 20 years because it did not address a problem of importance to conservation biology. However, that perception would change with time.

Conceptually, Levins envisioned a population separated into spatially discrete subunits ("habitat islands"). Individual population subunits suffered periodic and predictable extinction, but were recolonized by dispersers from neighboring subunits. Thus, population size was determined by the relationship between extinction and migration rates. If N represented the total number of local populations at a given time, T the total number of sites that could support populations, and m the migration rate (the probability that migrants from any given population can reach another site), then populations would be established as a product of the migration rate multiplied by the probability that the site reached was vacant:

$$mN\left(1-\frac{N}{T}\right).$$

For example, if the probability that migrants can reach another site is 50% per year ($m = 0.5$) and there are 100 populations ($N = 100$) living in an environment with 200 suitable sites ($T = 200$), then the annual number of migrations (50) times the probability of encountering a vacant site $\left(1-\frac{100}{200}\text{or } 0.5\right)$ is 25 (i.e., 25 new populations will be established annually). However, some populations are eliminated by local extinctions with a probability of E and a rate of EN. Thus, the change in the number of individuals in the population over time will be

$$\frac{dN}{dt} = mN(1 - N/T) - EN.$$

N reaches equilibrium, N_{eq}, when the right side of the equation is 0. Therefore, the population will reach equilibrium at

$$N_{\text{eq}} = T\left(1-\frac{E}{m}\right).$$

Persistence of the population requires that $m > E$, and equilibrium is reached at a population size at which E and m are equal. When the population is large, changes in the rate of extinction of subpopulations have relatively little effect. But if the population experiences a more general, overall decline, changes in E begin to have significant effects on population size. The value of E is almost certain to be variable because it will be affected by random environmental fluctuation. If E varies over time, then the value of N will never reach equilibrium, but rather will fluctuate within some range of values according to a given probability distribution. And if the extinction rate ever exceeds the migration (colonization) rate, the population will disappear (Levins 1969).

The Levins' model assumed that local (subunit) population dynamics were density dependent, that population dynamics in different patches were independent of one another, and that there was limited dispersal linking population subunits. Additionally, the original model assumed that all patches were of similar size and quality. There was no spatial correlation (clumping) of the patches, all patches were equally available to dispersers, the number of patches was very large, local populations were not affected by dispersal, and patches were modeled as either "occupied" (at carrying capacity) or "unoccupied" (no individuals in the patch) (Wiens 1996). The last assumption is the reason that Levins' model eventually came to be called the ***occupancy model*** (Gilpin 1996) to distinguish it from other types of metapopulation models that developed later.

The original Levins model represented a ***spatially implicit model*** of metapopulations. Its habitat patches and local populations were discrete, and all were assumed to be equally connected to one another (Hanski and Simberloff 1997). Spatially implicit models, because of their elegance and simplicity, facilitated mathematical and conceptual analysis of how metapopulations might work. Unfortunately, spatially implicit models were unrealistic, and their dependence on other assumptions about populations limited the questions that could be asked. As metapopulation theory

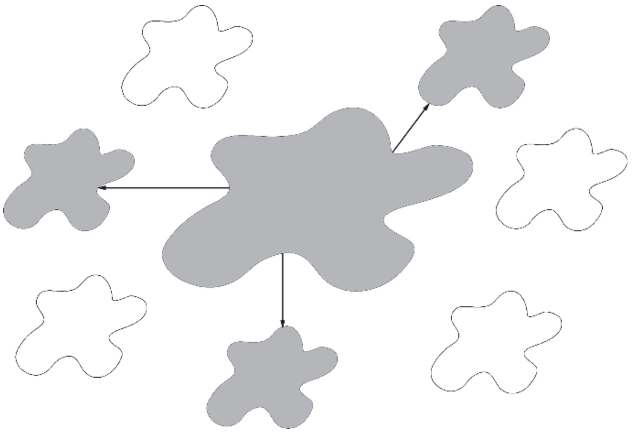

Figure 8.8. The mainland–island metapopulation model as proposed by Boorman and Levitt (1973). The Boorman–Levitt metapopulation consists of individuals inhabiting a large source area and several small sinks. The large "mainland population" is capable of supporting its own population in addition to supplying immigrants to smaller islands. Thus, the mainland serves as the primary source of inhabitants and is relatively extinction resistant. Arrows represent recolonization of sinks by individuals from the mainland. Open areas represent sinks in which extinction occurs without recolonization. Solid areas are source habitats that supply colonists. (Based on concepts described by Harrison 1991. Illustration by M. J. Bigelow.)

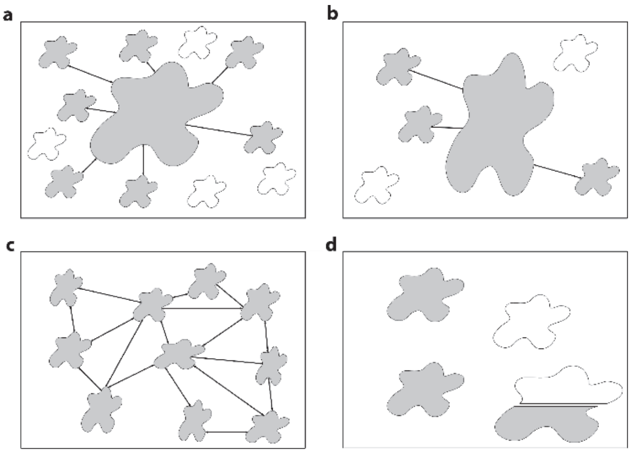

Figure 8.9. Metapopulation types. In a classical metapopulation (a), some colonies may not exhibit high rates of movement for long periods of time. Also, colonization may unite several patches within a larger patch and be united as a single entity that contributes to other sinks. Colonies farthest from the source are most prone to extinction. The mainland–island metapopulation (b) depicts local extinctions occurring mainly among a subset of populations. The mainland/source, resistant to extinction, functions as the major provider of colonists. The island and sink metapopulations have little affect upon regional persistence. In patchy populations (c), due to the high levels of emigration and immigration, the patches function as a whole unit. It is rare that discrete local populations become extinct. The absence or insufficiency of recolonization to balance extinction distinguishes non-equilibrium populations (d). Extinction of metapopulations occurs as part of an overall regional decline (i.e., a product of the reduction, fragmentation or deterioration of a habitat). (Based on concepts described by Harrison 1991. Illustration by M. J. Bigelow.)

and modeling continue to develop, they increasingly rely on two key premises: (1) populations are spatially structured into assemblages of locally breeding populations, and (2) migration among local populations has some effect on local population dynamics, including the possibility of population re-establishment following extinction (Hanski and Simberloff 1997). Subsequent to the development of the occupancy model of metapopulations (Levins 1970), Boorman and Levitt (1973) produced an alternative metapopulation model sometimes referred to as the "mainland-island metapopulation" model (Figure 8.8). In this model, one population subunit is significantly larger and more permanent than all others, and serves as the primary "source" population for smaller subunits. The "mainland" population never goes extinct. Therefore, the metapopulation never suffers extinction (Hanski and Simberloff 1997). Frequent dispersal from an extinction-resistant mainland to extinction-prone "island" populations prevents all small populations on the "islands" from suffering extinction at the same time (Harrison 1991).

Harrison (1991) elaborated a classification scheme for metapopulation models in four categories (Figure 8.9). Besides Levins' model (renamed the "classical model" by Harrison, Figure 8.9a) and the mainland-island model previously discussed (Figure 8.9b), Harrison proposed two other types of metapopulations. One is the "patchy" model, in which migration among subunits is so frequent that the patches function as a single demographic unit (Figure 8.9c). The other is the "non-equilibrium" model, in which movement among the subunits is so limited that each subunit functions as a separate population unit (Figure 8.9d). Extinction is not offset by recolonization, and the population suffers a long-term decline.

More recent efforts in the modeling of metapopulations have relied on ***spatially explicit models***, which assume differing degrees of connectedness between population subunits and feature "localized interactions." Localized interactions are those in which population subunits interact primarily or exclusively with neighboring subunits, not with all subunits. A further refinement in metapopulation modeling has been the development of ***spatially realistic models*** (Hanski and Simberloff 1997) that include considerations of the specific geometry of particular patches (especially on issues of size, shape, and arrangement of patches). Metapopulation theory's view of populations as spatially discrete subunits in fragmented, yet still connected, habitats offered a picture of what biologists perceived to be the case in nature. Biologists realized that any plan for maintaining extant populations would have to incorporate the preservation of many habitat fragments, rather than rely exclusively on large, contiguous habitat blocks. Further, conservationists perceived that population persistence also would depend on the ability of individuals to disperse successfully among habitats (McCullough 1996).

Metapopulation theory suggested that vacant habitats might be recolonized on a regular basis and unoccupied habitat could be as important as occupied habitat in long-term population persistence. Further, metapopulation theory suggests that a fragmented group of population subunits could actually enhance population structure and persistence (Simberloff 1997). As a result, spatial structure has become a key concept of metapopulation theory and modeling (Hanski and Simberloff 1997). Over time, modelers found they could relax the initial assumptions of the Levins (1970) model and make subsequent metapopulation models more realistic (Gilpin 1996).

8.3.3. A Metapopulation Case History: The Florida Scrub Jay

One species that has been used to classify, develop, and test metapopulation models is the Florida scrub jay (*Aphelocoma coerulescens*), Florida's only endemic bird (Figure 8.10). This species provides opportunity for metapopulation modeling because of its habitat requirements and natural history. Scrub jays are habitat specialists that prefer low growing, scrub-oak vegetation (*Quercus* spp.) interspersed with bare openings on sandy, nutrient-poor soils. Such habitat can be maintained only by frequent fires, and tends to be patchily distributed among large areas of other types of vegetation, unsuitable and uninhabited by jays (Woolfenden and Fitzpatrick 1984).

FIGURE 8.10. The Florida scrub jay (*Aphelocoma coerulescens*), a species that demonstrates a pattern of spatial distribution and population demography corresponding to the concepts and predictions of metapopulation theory. (Photo courtesy of Department of Environmental Services, Lake County, Florida (USA)).

Scrub jays are monogamous, cooperative breeders that establish well-defined territories in their preferred habitat. It is common for younger males to remain with the parents as "helpers" for one or more years rather than dispersing immediately. Such helpers typically increase the family's overall breeding success, help to expand territory borders, and increase their own chances of "inheriting" part or all of the parental territory in subsequent years (Woolfenden and Fitzpatrick 1984). Given this combination of reproductive behaviors and habitat preferences, Florida scrub jays are a textbook example of a metapopulation, a group of spatially discrete population subunits with high costs of dispersal among habitat patches.

Data on population distributions of the Florida scrub jay have revealed more complexity than traditional classification systems could incorporate. Stith et al. (1996) delineated 42 Florida scrub jay populations (Figure 8.11). Twenty-one of these were classified as "non-equilbrium" (small and extinction prone subunits), three conformed to the classical (Levins) model, three fit the "patchy" model of Harrison, and five matched the mainland-island model. To deal with new permutations seen in the remaining ten populations, Stith et al. (1996) added the category of "midland" subpopulations, groups that were not necessarily prone to extinction but were not invulnerable to extinction. With the addition of the midland category, Stith et al. (1996) categorized nine of the remaining ten populations as "midland-island" populations and one as a "mainland-midland" population. Further studies of *in situ* populations may benefit from insights gained by metapopulation modeling, but also are likely to provide additional examples of complex population structures that do not fit neatly into model classifications.

8.3.4. Managing Metapopulation Interactions: Implications of a Theoretical Model

Metapopulation dynamics may have significant effects on the conservation of populations through competitive interactions. For example, two competing species can coexist as metapopulations in the same patches even if one is competitively superior, as long as the inferior species can disperse more effectively or has a lower patch extinction rate (Hanski 1983, 1987). Nee and May (1992) modeled the effects of these competitive interactions in a patchy environment when patches were removed (i.e., when there was a decreasing amount of available habitat as a result of ongoing habitat destruction) (Figure 8.12).

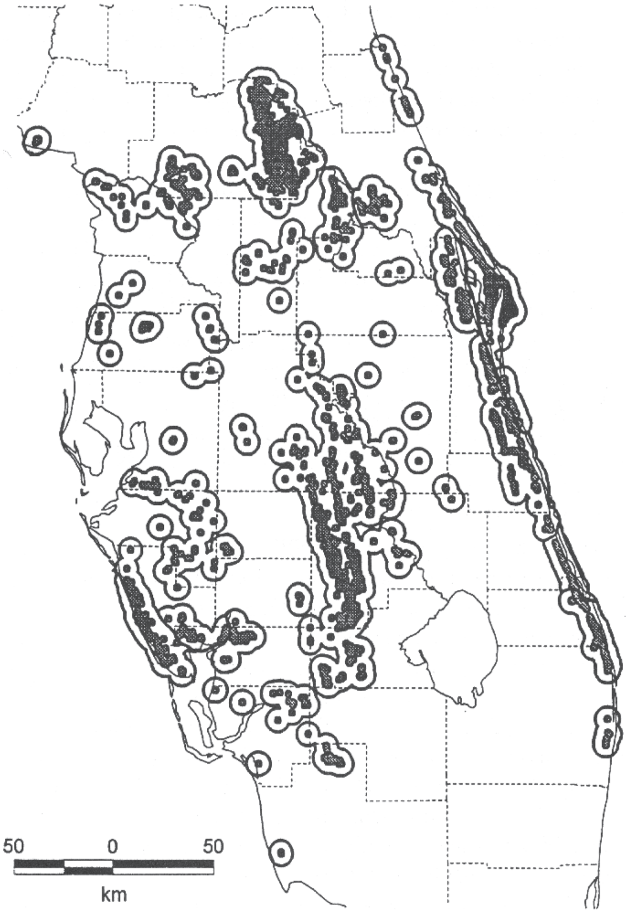

FIGURE 8.11. Florida Scrub Jay Metapopulation Distribution Map. This map depicts categories of population distributions of the Florida scrub jay and their relation to the conceptual models of metapopulations. Dark areas represent scrub jay subpopulations. The outer lines designate 42 separate metapopulations. (From *Metapopulations and Wildlife Conservation* by Dale R. McCullough, ed. Copyright 1996 by Island Press. Reproduced with permission of Island Press, Washington, DC.)

The fundamental question that Nee and May's model attempted to answer was: will habitat loss cause a change in community composition of patches that remain, even if these remaining patches undergo no changes? In this model, consider that a stock of habitat patches exist, some proportion of which are suitable patches for occupancy (*h,* for "habitable") while others may be unoccupied patches (*x*, the proportion of unoccupied patches). Suppose that species *A* is a superior competitor to species *B* such that if *A* invades a patch occupied by *B*, *B* is exterminated. Let *y* denote the proportion of patches occupied only by *A* and z the proportion of patches occupied only by *B*.

Recall from Levins' (1969) initial models of metapopulations that the persistence of metapopulations is defined by their migration rate from patch to patch (what Nee and May refer to as a "colonization rate") and their extinction rate. Let colonization and extinction rates be specific to *A* and *B* and equal to c_A, c_B and e_A, e_B, respectively. Then the rate of change in the proportion of unoccupied patches and the patches occupied by each species can be expressed through three equations.

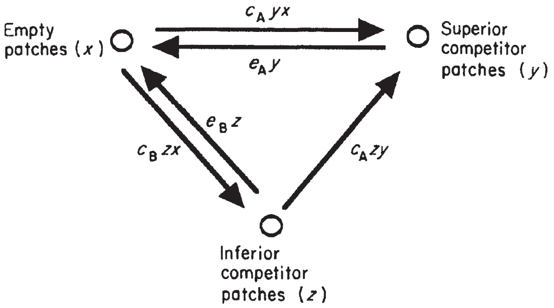

FIGURE 8.12. Patterns of colonization of empty and occupied habitat patches in an environment occupied by two competing species, A and B. A, the superior competitor, inhabits habitat y, and will eliminate B if it invades Bs habitat z. Note that, for A, colonizations in all types of patches are determined by the balance between colonization rate and patch extinction rates. For species B, this is true only for empty patches (x) because it cannot displace species A. Symbols are explained in text. (Nee and May, Dynamics of metapopulations: habitat destruction and competitive coexistence, *Journal of Animal Ecology*, Copyright 1992 by Blackwell Publishing.)

$$\frac{dx}{dt} = -c_A xy + e_A y - c_B xz + e_B z$$

$$\frac{dy}{dt} = c_A xy - e_A y + c_A zy$$

$$\frac{dz}{dt} = c_B zx - e_B z - c_A zy$$

These equations can be visualized in Figure 8.12. Note that for species *A*, sources of new patches can come from unoccupied patches or from patches occupied by species *B*, which it can exterminate. For species *B*, new patches can come only from empty patches.

As long as the proportions of empty (*x*), species *A*, (*y*) and species *B* (*z*) patches are not zero, the system can attain and persist at equilibrium (*x**, *y**, z*) and the proportions of unoccupied habitat (*x*), species *A* habitat (*y*) and species *B* habitat (*z*) have these solutions:

$$x^* = \frac{1}{c_B}(hc_A - e_A + e_B)$$

$$y^* = h - \frac{e_A}{c_A}$$

$$z^* = \frac{e_A(c_A + c_B)}{c_A c_B} - \frac{e_B}{c_B} - \frac{hc_A}{c_B}.$$

For species *B* to persist in this system the ratio of its colonization rate to its extinction rate must be greater than the equivalent ratio for species *A*. In other words,

$$\frac{c_B}{e_B} > \frac{c_A}{e_A}$$

This condition might be met if species *B* has a much higher rate of colonization than *A*, or a much lower extinction rate than *A*, or both.

When habitat destruction takes place (i.e., when the value of *h* declines), notice what happens to the system. The proportion of available habitat patches declines, and the proportion of habitats occupied by species *A* also declines. Perhaps what is surprising, and counterintuitive, is that the proportion of habitats occupied by the poorer competitor, *B*, actually increases because the negative term in the equilibrium equation, $\frac{hc_A}{c_B}$ is reduced. Consider the implications of the model's outcomes. If species *B* has persisted because it is a superior colonizer compared to *A* (i.e. *B* has a higher value of *c* than *A*), then the overall number of patches that *B* occupies will rise during periods of habitat loss. As Nee and May perceptively note, "When *h* falls below a critical value of its extinction colonization ratio ($h < e_A/c_A$), the superior competitor can no longer persist. Beyond this point, only the inferior competitor is found …" (Nee and May 1992). If habitat destruction continues, the inferior competitor also will decline and eventually perish.

The implications of this model are insightful and, perhaps, troubling. For one thing, it is not necessary to destroy all available habitat to exterminate any single species that exists as a metapopulation, persisting through a balance of colonization and extinction in disjunct habitat patches. Perhaps more disturbing is that, if conditions of this model are met, patch removal has significant and surprising effects on population levels of competing species. Removing habitat patches may actually increase the proportion of remaining patches occupied by the poorer competitor. Thus, the observation that habitat loss and fragmentation may favor "weedy" species at the expense of more specialized species (species that are often of greater concern in conservation) may not be due entirely to the effects of disturbance or to increasing the amount of edge. Disruption of competitive relationships also may play a significant role.

POINTS OF ENGAGEMENT – QUESTION 1

If the conditions of this model are met in the real world, what would happen to the populations of two such competing species if habitat patches were *added* (such as converting croplands from production to prairies)? Design a field experiment that might evaluate predictions of this model. Specifically, what would be your research hypothesis, your experimental treatment and control, and your test consequence?

8.4. Population Viability Analysis

8.4.1. Conceptual Foundations

Because the problem of species extinction was a compelling concern in the genesis of conservation biology, a critical question emerged: in a world of limited resources for conservation and many socio-political boundaries, what was the minimum number of individuals needed in a population to ensure its survival? As noted earlier, the first attempts to answer this question were rules of thumb based on genetic considerations. Franklin (1980) asserted that inbreeding is kept to a tolerable level in populations with an effective size of 50 or more individuals and that effective populations of 500 or more tend to retain acceptable levels of heterozygosity. Franklin stated that "in randomly mating populations, such as are found in most mammals and birds, inbreeding considerations alone require that population numbers should be not less than 50 individuals." Other investigators found that greater threats to small populations lay in problems associated with random variation in birth rates, death rates, and other demographic variables (demographic stochasticity) and the effects of random environmental variation on the population's rate of increase (environmental stochasticity). Both demographic and environmental stochasticity often had increasingly deleterious effects on populations as the population declined in size.

The sense of duty conservation biologists feel to conserve endangered species is impossible to fulfill without the ability to conserve them. The lack of reliability, precision, and sensitivity to the demographics and environments of individual populations inherent in genetic rules of thumb did not provide that ability, and motivated the search for more precise and comprehensive estimates of minimum population thresholds needed for population persistence. Out of this need arose the concept of the ***minimum viable population*** (Shaffer 1981), or MVP, as an estimate of the minimum number of individuals needed for the population to survive for a given period of time with a specified probability of persistence. Some common conventions that emerged for minimum viable populations were the minimum population size that had a 95% probability of persistence for 100 or 1,000 years. The belief that some discrete minimum viable population can be calculated for individual species has been largely discredited and abandoned in conservation biology, and has been replaced with projections of the ***persistence likelihood*** of a population, an estimate of the probability of persistence or extinction that has been refined with the development of the technique called ***population viability analysis***, or PVA, in which analytical or simulation models generate precise estimates of the likelihood of species persistence within a defined time period at a given level of probability (i.e., uncertainty). PVA models, especially models for individual species, quantitatively evaluated factors of extinction risk and were able to provide estimates of the probabilities of essential stochastic events in populations (Groom and Pascual 1998).

Precisely defined, population viability analysis is *the estimation of extinction probabilities by analyses that incorporate identifiable threats to population survival into models of the extinction process* (Lacy 1993). PVA is a form of risk-assessment whose goal is to evaluate whether a population will fail or prosper in response to specific conditions and, more particularly, an assessment of extinction risk over a specific time horizon under a given set of circumstances. PVA is an application of population modeling that estimates the effects of environmental and demographic processes on population growth rates. These models also can be used to estimate probabilities of a population falling below a certain level. This information is helpful in understanding the threat of a species' extinction from environmental and demographic factors.

PVA-based models are data demanding and require thorough understanding of the life stages of the species of interest, as well as careful ecological modeling. PVA models assume that enough is known about the population's ecology, dispersal, demography, genetics, and distribution to make an accurate estimate of the probability of persistence or extinction. This assumption is not always true. Nevertheless, such models attempt to predict patterns of population change over time as well as estimate the probability of population persistence under specified conditions. In addition, PVA-based models have value in their capacity to explore potential causes of population decline and potential routes to recovery, estimate the relative strength of different threats to population persistence, and discover the importance of neglected aspects of population demography. Model building or model analysis can guide the investigator to greater insights about the system, reveal previously unsuspected interactions, and illustrate unsuspected dimensions of a population's demography or environment. Collectively, these attributes are referred to as *heuristic* benefits of modeling, and may be at least as important as the model's final results or predictions. Such heuristic benefits of model building and analysis help to develop and evaluate hypotheses regarding causes of population increase or decline as well as evaluate the relative effectiveness of various management options (Beissinger and Westphal 1998).

Models are especially helpful when managing small populations common to threatened and endangered species because direct experimental manipulation would have low statistical power (insufficient numbers of individuals and groups) and unacceptable risk (high probability of losing some individuals of an already small population in experimental treatments). However, field studies remain essential for an accurate understanding of the population demography of small populations as well as for their effective management because PVA models cannot replace field studies and experiments needed to test hypotheses generated by modeling efforts.

Population models may be classed generally as *deterministic* (model elements do not vary across time) or *stochastic* (model elements vary through time). Although stochastic models are more challenging to build and interpret, they more accurately reflect population behavior because demographic processes are inherently variable.

As noted earlier, small populations are at much higher risks of extinction from random events associated with environmental and demographic stochasticity, genetic drift, and natural catastrophes. Therefore, PVAs normally do not allow a population to reach a level of zero (actual extinction), but rather specify a lower limit or extinction threshold, below which extinction would be nearly certain due to these same forces. This "quasi-extinction threshold" is then built into the model as a fixed and limiting parameter.

The output of a PVA can be in one of four forms. If the quasi-extinction threshold and the time horizon are both allowed to vary, the output takes the form of a three-dimensional "quasi-extinction surface" in which time to threshold, extinction threshold, and probability of dropping to or below the threshold are plotted simultaneously. If time is fixed, the output produced is a two-dimensional "quasi-extinction curve" in which different numerical thresholds are plotted against different quasi-extinction probabilities. Or, if the quasi-extinction threshold is fixed (for example, the manager determines that the population must never drop below 200 individuals), then the output generated is a probability distribution of different extinction times. This kind of output is used to find the mean or median value of the probability distribution. A fourth approach to output is to run multiple simulations with defined thresholds, defined times, and defined probabilities. Such an approach produces a series of curves known as "quasi-extinction contours" that reveal, for a given quasi-extinction probability, a combination of time and threshold associated with it (Figure 8.13) (Groom and Pascual

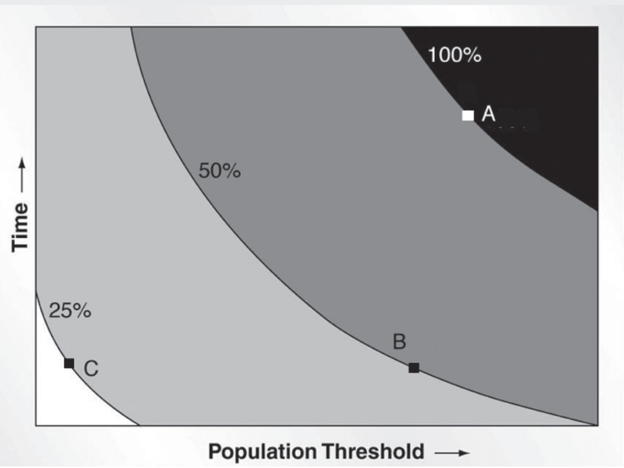

FIGURE 8.13. An example of quasi-extinction contours generated from a population viability analysis (PVA). Each point on a given curved line (contour) represents a combination of time and population size having a given probability of quasi-extinction (reduction of the population to such a low level that extinction is nearly certain) such that all points on the same line have equal quasi-extinction probabilities. (Based on concepts from Ginzburg et al. 1982. Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications,* Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

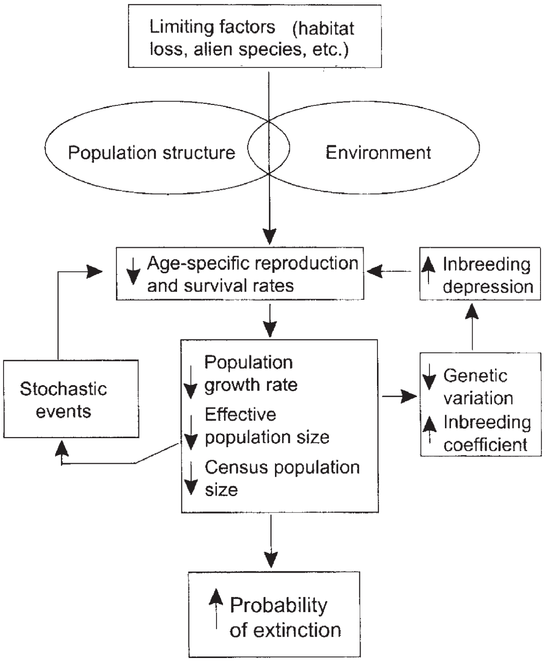

FIGURE 8.14. Simplified representation of an "ideal" Population Viability Analysis (PVA) model, including interaction between population structure and environmental variation to affect demography, population growth rates, and probability of extinction. The population's age structure, sex ratio, behavioral interactions, distribution, physiological status, and age specific birth and death rates are modeled as components of population structure. Arrows within boxes indicate an increase or decrease. (*Population Viability Analysis.* K. Ralls, S. R. Beissinger, and J. F. Cochrane. S. R. Beissinger and D. R. McCullough, editors. Copyright 2002 by the University of Chicago.)

1998). An "ideal" PVA combines all of the features thus far described, beginning with an accurate identification of the limiting factors constraining the population (Figure 8.14). In one way or another, the model establishes connections between the population and its environment, and couples those interactions to their effects on age-specific reproduction and survival rates, which are treated as stochastic rather than deterministic events. Genetic variation and effects of inbreeding are also modeled and coupled to reproduction and survival. The model's output is an estimate of the probability of extinction of the population under different scenarios of environmental and demographic events (Ralls et al. 2002).

8.4.2. Uses of PVA Models

The use of PVAs has increased dramatically since their inception. Groom and Pascual reviewed 58 PVAs published in major conservation journals from 1987 to 1996. In the first 5 years, there were only 10 (17%), whereas the second 5 years saw 48 such publications (83%) (Groom and Pascual 1998). The US National Research Council (USNRC) has recommended even greater reliance on PVAs for the management and conservation of endangered species (US National Research Council 1996) and that recommendation has been manifested in the increasing numbers of studies that have used PVA since the USNRC review was completed (Henle et al. 2004). Although PVAs are increasingly used in both research and management in general ways, they still have a relatively small role in actual management plans for endangered species. In the US, for example, less than 20% of 86 recovery plans developed by the US Fish and Wildlife Service for threatened and endangered species between 1992 and 2002 used PVAs (Shaffer et al. 2002).

PVAs also have shifted in their expressed purpose of use. The majority of the earliest publications were designed to determine optimum harvest levels (1987–1989), but, since 1990, the most common uses have been determining the viability of populations, particularly of threatened and endangered species, and for conservation management. Today PVAs typically are created to accomplish one or more of four basic objectives: (1) organize existing data about a population of conservation interest; (2) estimate the relative risk to the population of different environmental and demographic factors; (3) estimate the absolute risk to the population of these factors; and (4) manage the population adaptively by comparing model predictions to actual population behavior and, from such comparisons, continue to work to improve the model through ongoing experiments and monitoring (Ralls et al. 2002). In trying to accomplish these tasks, PVAs can be categorized in multiple ways. A broad dichotomy exists between analytical-deterministic and stochastic PVAs. Analytical-deterministic models are usually also "structured" PVAs, dividing (structuring) the population into ages, classes, stages, or sizes that have values of demographic variables specific to such divisions (Groom and Pascual 1998). Such structured PVAs make a deterministic projection of the population's growth, size, and trajectory into the future. In theory, deterministic or analytical PVAs can provide the most accurate estimates of population viability, provided that all needed data are available and measured with little or no error; however, these two conditions are rarely met, especially in small and endangered populations. In addition, remember that precision is not the same as accuracy. Most biological processes are stochastic in nature, and outcomes are inherently uncertain. Models that fail to express the degree of uncertainty are prone not only to error but to serious misinterpretation. As J. Maynard Smith, speaking of biological modeling long before the advent of PVAs, stated with no equivocation, "the use of deterministic rather than stochastic models can only be justified by mathematical convenience" (Maynard Smith 1974). Thus, the second category of PVAs, stochastic simulation models, has become the approach of choice and widest acceptance by the professional community. Stochastic simulation models also may be structured, in which case a different probability distribution for basic demographic variables (reproduction, growth, mortality) may be assigned to each group or class.

PVAs also may be spatially explicit or non-spatial. The model may assume that the population enjoys a common distribution throughout a given environment (non-spatial), or that it exists as separate subpopulations that are spatially disjunct from one another (spatially explicit). Non-spatial PVAs are more common, primarily because they are easier to model. Non-spatial PVAs do not, for example, require information on migration rates, but spatially explicit PVA models do, and their predictions are strongly affected by even small errors in this variable. Spatially explicit PVAs also require subgroup-specific data on population demography in order to model the persistence of subgroups as independent events. Obviously, subdividing a single population into multiple subunits means that each subunit consists of a smaller number of individuals, making the subunits more susceptible to extinction-causing processes, especially to the effects of demographic stochasticity. Such subdivision tends to decrease effective population size and have a negative effect on the projected viability of the population. Thus, most spatial models tend to predict lower population viability than non-spatial models of the same population (Groom and Pascual 1998). Spatial PVAs, when properly designed and given accurate data, can make more accurate projections about populations that experience complex interactions with their environment and can evaluate the persistence of metapopulations. However, they demand labor-intensive collection of field data, as well as increased computer space and running time, making them a minority among published PVAs to date.

Most PVAs used today also have some means of modeling density dependent effects on population processes. The simplest approach is to have density independent growth up to a ceiling value (carrying capacity), and allow no growth once this level is reached. More sophisticated, and more biologically realistic approaches permit the value of the carrying capacity to vary stochastically, define a growth function that decreases in strength as population size approaches carrying capacity, or both. Some models also permit the modeler to reduce other (non-reproductive) vital rates in populations as carrying capacity is approached. Stage-specific PVAs also may have stage-specific differences in density dependent functions. Finally, some PVAs create density dependence through spatial structuring. For example, a PVA may be spatially explicit in terms of animal distribution. A minimum space requirement for breeding, such as a territory, can then effectively limit population size and create area-related density dependent effects in population processes. Spatially explicit PVAs can also regulate density through assumptions about the effects of density on dispersal.

PVAs are increasingly popular, but not all PVAs are reliable. To understand more about how a PVA really works and, therefore, to understand what makes a particular PVA reliable or unreliable, we will now examine in detail how a simple PVA could be constructed using a threatened North American plant, the western prairie fringed orchid.[1]

POINTS OF ENGAGEMENT – QUESTION 2

The US Endangered Species Act rarely provides protection before a population drops to such low levels (<1,000 individuals) that random demographic and environmental forces may lead to extinction even with complete protection. What criteria would you use to identify declining populations in need of protection before they reach this point?

8.4.3. A Stage-Based Deterministic Model – The Western Prairie Fringed Orchid

8.4.3.1. General Considerations

Many species of plants and animals have life cycles with distinct ages, stages, or sizes that influence population growth (Ebert 1999). In some cases, reproduction occurs only when organisms reach a certain age. The same may be true for mortality. In others, demographic events are structured by body size classes, or there are distinct growth forms of life "stages" that each have unique, stage-specific demographic rates. Further, the probability of remaining in the same stage (stasis) or transferring to another stage strongly affects the observed pattern of population growth. A generalized way of understanding such stage-based transitions can be seen in Figure 8.15. As you can see from the figure, all three kinds of life histories are variations on a common theme. To attempt population viability analysis of organisms with this pattern of life history, we must create a model in which age-, size-, or stage-specific demography and transition rates are known and properly related to one another. This requires the construction of the "stage-based" population model.

As a test case, we will use an approach developed by population biologist Carolyn Sieg and biostatistician Rudy King of the US Forest Service in considering the problem of building a model of population viability analysis for the western prairie fringed orchid (*Platanthera praeclara*), one of only a few threatened species in the US in which adequate long-term census and demographic data permit development of an accurate and detailed species PVA (Samson 2002; Sieg and King 1995). The western prairie fringed orchid is a US federally designated threatened plant species in which individuals pass through and among different life stages (Sieg et al. 2003a, b, c, d). In ecology

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[1] Material on the PVA for the western prairie fringed orchid was originally developed by Carolyn Sieg, Rudy King, and Fred Van Dyke for exercises in *A Workbook in Conservation Biology: Solving Practical Problems in Conservation* (Sieg et al. 2003a, b, c, d)

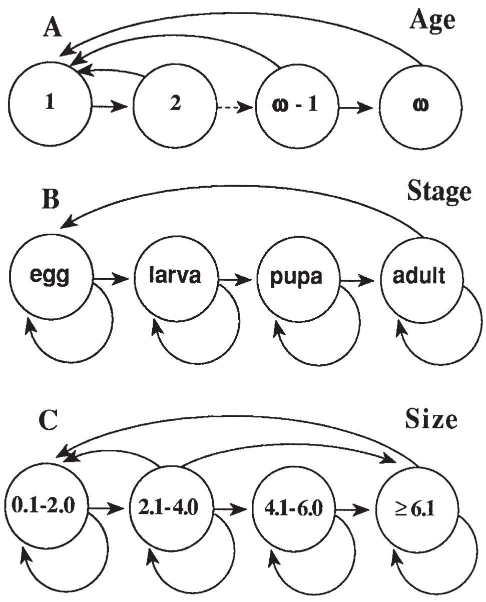

FIGURE 8.15. (A) Age-structured life cycle of a species with transitions (probabilities of survival) from one age to the next with return transitions to age 1, which are reproductive contributions; ω is the final age class and no individuals survive past this age. (B) Stage-structured life cycle of an insect; during a given time period, individuals may remain in a stage or transfer to the next stage. (C) Life cycle of a species whose demographic events are structured by size classes showing some of the possible transfers including shrinking to a smaller size and skipping a size class. (Ebert 1999. Copyright 1999 by Elsevier.)

and natural history, the western prairie fringed orchid is a wetland species that was once locally common west of the Mississippi River in the tallgrass prairie biome (US Fish and Wildlife Service 1996). With settlement of this region, more than 80% of the native prairie has been converted to cropland or otherwise developed (Klopatek et al. 1979), and many of the region's wetlands have been drained or significantly altered (Dahl 1990). As a result, the orchid has disappeared from nearly 75% of counties where it once was documented, and in 1989 was listed as a threatened species (US Fish and Wildlife Service 1989). The largest potential metapopulations of the orchid occur in the northern United States and southern Canada (Figure 8.16) (US Fish and Wildlife Service 1996).

FIGURE 8.16. Historic distribution of the western prairie fringed orchid (*Platanthera praeclara*) in the central United States and southern Canada, and the three largest remaining metapopulations (solid dots) of greater than 3,000 plants each. (Map courtesy of US Fish and Wildlife Service 1996.)

FIGURE 8.17. Life stages of the western prairie fringed orchid (*Platanthera praeclara*) including vegetative stage (a), reproductive flowering adult (b), and protocorm and seedling stage (c). (Photos courtesy of Carolyn Hull Sieg (a and b) and Verla J. Nicholas (c).)

Only a small portion of the area on which orchid populations persist is managed specifically for orchid protection. On most areas, multiple land use activities, including surface water and groundwater diversion, livestock grazing, prescribed burning, production of hay, and wetland drainage to allow farming are common and expected to continue. Some land management activities, depending on their timing and intensity, may be beneficial to the orchid by removing competing vegetation. Other land management activities, such as wetland drainage, are rarely beneficial. Thus, a thorough understanding of orchid life history is prerequisite to exploring possible future population trajectories, as well as evaluating the relative differences among effects that land use activities may have on population persistence.

The life history of the orchid includes two distinct aboveground stages. Vegetative plants are usually short (<15 cm), and have only one or two leaves (Figure 8.17a). Flowering plants are most conspicuous, growing up to 1.2 m tall, and producing a beautiful branched flowering stalk with numerous cream-colored flowers (Figure 8.17b). The lower petal of each flower is deeply three-lobed and fringed, hence the orchid's common name. When successful pollination occurs, flowering plants may produce thousands of dust-like seeds (Hof et al. 1999). The next growing season, the seeds develop into an underground structure called a protocorm, which relies on mycorrhizae for its sustenance (Figure 8.17c). In time, the protocorm develops into a seedling and as the plant emerges from the ground it begins to photosynthesize. Germination, protocorm development and transition to a seedling can occur within one growing season.

8.4.3.2. Stage-Based Deterministic Models

Recovery efforts for rare species, especially plants like the western prairie fringed orchid, require a thorough understanding of all life-history stages, as well as detailed information on transition rates between stages. The Lefkovitch, or stage-based model (Lefkovitch 1965) is used for many species of plants, as well as many species of fishes and invertebrates, whose demographic rates are better related with development stage than age. The first step in developing a stage-based model is to identify the life-history stages of the species and the pathways of transition among the stages. Transition probabilities are then calculated from field data collected over several years. Matrix algebra is used to calculate several useful statistics (Burgman et al. 1993), such as lambda (λ), or the geometric rate of increase. λ is the ratio of the population in year 2 to the population in year 1 ($\lambda = N_2/N_1$). A population in which the estimated $\lambda = 1.0$ is stable. When λ is >1, the population is increasing. When λ is <1, the population is declining. The value of λ provides a measure of the rate of increase or decline. For example, a population with $\lambda = 1.12$ is growing at a rate of 12% per year, whereas a population with $\lambda = 0.97$ is decreasing at a rate of 3% per year.

8.4.3.3. Constructing the Model and Matrices

8.4.3.3.1. Life-History Stages and Their Parameters

The first step in developing a demographic model is to identify the life-history stages of the organism, in this case the orchid. For example, the generalized life stages of an annual plant might include: vegetative plant, flowering plant, and seeds, which could be displayed as a simple arrangement of rows and columns. Let *P* represent any within-stage transition, or the probability that the plant will remain in the same stage. *G* (growth) values represent transition probabilities from one stage to another, and *F* (fecundity) is the number of seeds produced by a flowering plant. Subscripts represent the column (first number) and row (second number). Thus, P_{11} is the probability that a seed will remain viable in the soil. G_{12} is the probability that a seed will germinate and become a vegetative plant, G_{23} is the probability that a vegetative plant will flower, and F_3 is the number of seeds that a flowering plant produces. This simple model could then be displayed in a matrix that summarizes the life stages and transitions:

	Present life stage		
Next life stage	Seeds	Vegetative plant	Flowering plant
Seeds	P_{11}	–	F_3
Vegetative plant	G_{12}	–	–
Flowering plant	–	G_{23}	–

Suppose for our hypothetical annual plant we have data from 650 vegetative plants that were marked and monitored in the field for 3 years. Of these 650 vegetative plants, 320 flowered. Further suppose that we measured seed production of 50 flowering plants, and over the 3 years, the average seed production per plant was 23, of which 45% are viable.

We might not have data on germination rates of the seeds, but let us assume that 10% of the seeds germinate, and 20% of the seeds remain viable in the soil seedbank. Using these data, we could calculate appropriate values for our ***transition matrix***, replacing the general expressions we previously used with real probabilities. Some cells might have no values because some transitions do not actually occur (for example, vegetative plants do not revert to seeds). But, where transitions do occur, the transition matrix would look something like this.

	Present life stage		
Next life stage	Seeds	Vegetative plant	Flowering plant
Seeds	(0.2)	–	23(0.45) = 10.35
Vegetative plant	(0.1)	–	–
Flowering plant	–	320/650 = 0.49	–

Thus, the first step in developing a model for the western prairie fringed orchid requires identifying the life stages of the orchid and then developing a transition matrix that estimates the probabilities of an individual moving from one life stage to the other.

8.4.3.3.2. Constructing Transition Matrices for the Western Prairie Fringed Orchid

To identify all the transitions in the life history of the orchid, additional information is needed. The western prairie fringed orchid is a perennial plant that may persist for several years in some locations. A vegetative plant in year 1 may remain vegetative in year 2, become a flowering plant, or disappear. Likewise, a flowering plant in year 1 may be vegetative or flower in year 2, or it may disappear. The plants that disappear may be dormant, or they may be dead. One could now construct a diagram similar to the one displayed earlier in Figure 8.15, but in this case showing the life stages of the western prairie fringed orchid, drawing arrows on the diagram to indicate transitions. It would look something like the one displayed in Figure 8.18. The protocorm/seedling stages are combined into one matrix

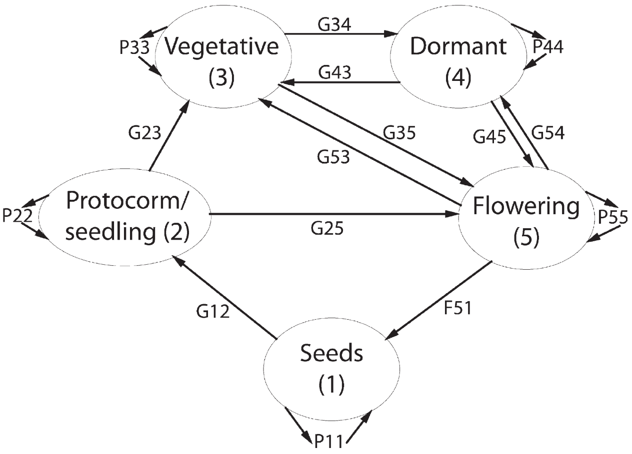

FIGURE 8.18. Visual representation of the life-history stages and transitions of the western prairie fringed orchid (*Platanthera praeclara*). *P* variables represent probabilities of remaining in the same stage (stasis probabilities), *G* variables represent transition rates between life stages, and F_5 represents the fecundity rate (seed production) of flowering plants. (Concept by F. Van Dyke. Drawing by M. J. Bigelow.)

element because growth from protocorm to seedling can occur within one growing season.

Using the diagram as a guide, we could now construct a transition matrix for the orchid. For example, the probability that a seedling in 1 year becomes a vegetative plant in the next year would be designated as G_{23}. Some cells in the matrix will have no values because some transitions never occur. From this generalized, theoretical format, we could now add real, empirical data gathered from *in situ* studies of the orchid population. To complete the transition matrix for the western prairie fringed orchid with real values, we would need detailed data on both aboveground and belowground transitions. For the aboveground data, we could use data collected over 5 years on 16 sites on the Sheyenne National Grassland in southeastern North Dakota, USA (adapted from Sieg and King 1995). Beginning in 1990, vegetative and flowering plants in 16 belt transects were permanently marked and numbered. Each year the status of previously marked plants was recorded, and any new plants were marked. With this data, we could calculate the transition probabilities for a vegetative plant becoming a flowering plant in the following year, and calculate the overall average for 4 years.

	Number of vegetative plants in year 1	Number of vegetative plants that flowered in year 2	Probability of a vegetative plant flowering in year 2
1990–1991	74	0	0.00
1991–1992	54	10	0.185
1992–1993	154	53	0.344
1993–1994	361	12	0.033
Average			$0.141 = G_{35}$

8.4.3.3.3. Estimating Fruit Set

Sieg and King estimated fruit set by permanently marking 635 flowering plants between 1995 and 1998 (Sieg and King 1995). At the end of each growing season, the number of plants that produced viable fruits was recorded, as was the number of viable fruits per plant. If we assumed that each flowering plant produced an average of 1.2 fruits per plant and each fruit produced an average of 21,618 seeds, of which an average of 53% were viable (Hof et al. 1999), we could calculate the average number of viable seeds produced per flowering plant. The expression would take this form,

$$(1.2)(21{,}618)(0.53) = 13{,}749 = F_5.$$

and we could now complete the matrix. The other aboveground data could be calculated similarly. Sieg and King also estimated the probability of seedlings becoming vegetative and flowering plants based on the appearance of new plants. Using data from seed packets buried in the ground and then retrieved the following year, Sieg and King approximated transition probabilities for seed germination rates and development into protocorms and seedlings (Hof et al. 1999). Assuming that protocorms do not persist beyond 1 year, we could now complete the matrix as follows:

Status next year	Present status				
	Seeds	Seedling	Vegetative	Dormant	Flowering
Seeds	P_{11}	–	–	–	$F_5 = 13{,}749$
Seedling	G_{12}	P_{22}	–	–	–
Vegetative	–	0.0301	0.2806	0.0815	0.2106
Dormant	–	–	0.5783	0.1015	0.6968
Flowering	–	0.0099	0.1411	0.0299	0.1025

Sieg and King did not have empirical data on seed viability in the soil, but arbitrarily assumed that 50% of the seeds produced remain viable in the soil. Thus, the resulting matrix is:

Status next year	Status this year				
	Seeds	Seedling	Vegetative	Dormant	Flowering
Seeds	0.5	–	–	–	$F_5 = 13{,}749$
Seedling	0.0015	0.00	–	–	–
Vegetative	–	0.0301	0.2806	0.0815	0.2106
Dormant	–	–	0.5783	0.1015	0.6968
Flowering	–	0.0099	0.1411	0.0299	0.1025

We have worked through this example slowly and in some detail in order to allow you to re-create the intellectual process through which a population viability analysis could actually begin to be created, beginning with the determination or estimation of all the transition probabilities associated with the life history of the species. Conservation biologists who develop PVAs or attempt to interpret their results need a thorough understanding of this process, first, in order to conceive of how to do empirical research on populations that will yield the kind of data needed for population viability analysis, second, to know how to determine transition probabilities for a population model from empirical data, and third, to be able to intelligently understand and interpret the results of any PVA, such as one might find in a scientific journal. But before we begin the work of interpreting an actual study, we have more work to do on the orchid model.

8.4.4. The Concept and Use of Elasticity in PVA Analysis

Understanding how to translate PVA results into meaningful management actions and strategies requires that we know which variables most affect the viability of the population and, if possible, why. For example, large changes in some variables might have little or no effect on population persistence, while very small changes in other variables might have large effects on population survival. The variable or variables that have the greatest proportional effect on λ are those that should be most intensely managed. Mathematically this would be expressed as

$$\partial\lambda / \partial a_i,$$

which is the change in λ associated with change in life history trait a_i, in other words, the partial derivative of λ with respect to a_i. Thus, the value of $\partial\lambda/\partial a_i$ is really a measure of the amount of change in λ that can be attributed to the variable a_i, which is by definition a measure of the *sensitivity* of the population's growth rate to that variable.

The expression $\partial\lambda/\partial a_i$ is a measure of the absolute selective pressure of a variable on population growth. A more common and effective way to assess this effect is to express such sensitivity in proportional terms. By definition, the proportional sensitivity of matrix elements is called ***elasticity*** (e_i), and can be expressed as

$$e_i = \frac{\partial(\ln\lambda)}{\partial(\ln a_i)}$$

Elasticity is a type of sensitivity analysis that refers to the effect of a variable on model outcomes (Burgman et al. 1993). In general, any sensitivity analysis of a PVA evaluates how changes in life-history attributes of the model affect population growth or rates of extinction. In an elasticity analysis, the greater a variable's elasticity, the more a change in the value of the variable will change the value of λ, the population's rate of growth (de Kroon et al. 1986). Elasticity analyses can provide insights on identifying potential management strategies for threatened populations because they can identify which matrix element to change that could provide the quickest route to population recovery (Beissinger and Westphal 1998), and they are also vital when the value of key model parameters is uncertain because they tell the modeler how much such uncertainty matters. Today, PVA models are usually programmed to automatically generate the elasticity values of each variable, but it is the biologist who must know how to use and interpret them. The larger a variable's elasticity value, the greater its effect on population viability. Elasticity analyses are useful in the assessment of population viability in at least four ways. First, they aid in understanding which variables are important for populations projected to increase compared with those projected to decline. Second, elasticity values allow examination of our basic assumptions about population persistence and help us understand whether areas of uncertainty in the model are important or unimportant to population performance. For example, if we believe that seed germination rates are the key to the persistence of the western prairie fringed orchid, but discover that we can manipulate the model's germination rates over a wide range of values and see little effect in population growth, we are led to re-examine our assumption. We also learn that, despite our uncertainty about germination rates, it really does not matter much. Third, elasticity analysis permits managers to identify the variables to focus on in developing management guidelines, which will be those with highest elasticity. Fourth, an elasticity analysis helps to identify future research needs. If we find variables with high elasticities, but have no idea why they are affecting population persistence as strongly as they are, we must organize future research efforts around examining these variables to gain a better understanding of their role in the population's growth.

8.4.5. Stochastic Models

In deterministic models, transition probabilities are held constant throughout the projected time period and populations are allowed to increase without bound (Beissinger and Westphal 1998). Deterministic models are mathematically convenient, but biologically unrealistic. Because most biological processes are stochastic, stochastic models, properly constructed, may more accurately represent real population dynamics.

To incorporate the array of variation in nature that can influence population growth, stochastic models contain many elements that deterministic models do not. For example, stochastic models can incorporate the variability inherent in annual rates of reproduction and death (demographic stochasticity) as well as climatic changes, such as wet and dry years (environmental stochasticity), which in turn influence demographic rates. Further, stochastic models often incorporate the concept that habitats have a maximum carrying capacity – that is, there is a limit to the number of individuals that they can support. A "population ceiling" may be invoked in the model to designate an upper numerical limit beyond which the population cannot grow (Burgman et al. 1993). Stochastic models may also incorporate probabilities for uncommon environmental events (catastrophes) that may have disproportionately severe effects on population numbers. In the western prairie fringed orchid, we could incorporate standard deviations associated with aboveground demographic transitions, allowing us to place confidence intervals around our population projections. In addition, we could impose a ceiling on the maximum population of flowering orchids, and use 1,000 iterations of the model so that an average percentage of population projections of <50 individuals could be calculated. Assuming that populations of less than 50 individuals have a low probability of persisting, this estimate will provide us with a measure of the probability of "quasi-extinction," a valuable concept we have discussed earlier representing a level below which we would not want the population to drop (Groom and Pascual 1998). Finally, to make the model even more realistic, we could incorporate the occurrence of three climatic scenarios (average, wet and dry) to project population growth rate and persistence under different environmental conditions. Outcomes would differ in each case (Table 8.2). Now, let us take these knowledge and skills one step further, and use them to interpret and assess the published results of a study of another endangered plant, the Arizona cliffrose (*Purshia subintegra*), in which investigators developed a PVA model using a similar, stage-based approach.

8.4.6. The Arizona Cliffrose: PVA Analysis of an Endangered Species

In the United States, the Arizona cliffrose is a federally listed endangered species of shrub native to central Arizona. The Arizona cliffrose is a habitat specialist that grows on limestone outcrops in the upper Sonoran desert vegetation zone, a "cold desert" ecosystem dominated by desert-adapted shrubs, and is now reduced to four populations in Arizona's Verde Valley. In addition to habitat loss, the Arizona cliffrose is expected to be further threatened in coming years with increasingly hot and dry conditions in its range associated with global climate change. In this setting, Joyce Maschinski and her colleagues developed a stage-based population model for use in a population viability analysis of this plant, not only to assess the general prospects for the survival of the species and possible management strategies for its recovery, but even more specifically to model expected effects of climate change on population persistence in an endangered species (Maschinski et al. 2006).

Like the model for the western prairie fringed orchid, the model for the Arizona cliffrose also contains five

TABLE 8.2. Output of a PVA of the western prairie fringed orchid (*Platanthera praeclara*), showing changes in numbers of individuals over time under average, wet, and dry climate conditions.

Average				Wet				Dry			
Time step	Flowering plants	Flowering plants λ	Percent of iterations below 50 flowering plants	Time step	Flowering plants	Flowering plants λ	Percent of iterations below 50 flowering plants	Time step	Flowering plants	Flowering plants λ	Percent of iterations below 50 flowering plants
0	250			0	250			0	250		
1	158	0.63	0	1	382	1.53	0	1	20	8.08E-02	100
2	98	0.62	0.1	2	313	0.82	0	2	10	0.49	100
3	111	1.13	0	3	310	0.99	0	3	39	3.93	100
4	121	1.09	0	4	413	1.33	0	4	22	0.57	100
5	116	0.95	0	5	549	1.33	0	5	13	0.56	100
6	110	0.95	0	6	664	1.21	0	6	12	0.92	100
7	108	0.98	0	7	780	1.18	0	7	9	0.76	100
8	106	0.98	0	8	934	1.2	0	8	6	0.69	100
9	103	0.97	0	9	1,136	1.22	0	9	5	0.76	100
10	100	0.97	0	10	1,382	1.22	0	10	4	0.76	100
11	98	0.98	0	11	1,674	1.21	0	11	3	0.74	100
12	95	0.97	0	12	2,014	1.2	0	12	2	0.74	100
13	93	0.97	0	13	2,424	1.2	0	13	1	0.75	100
14	91	0.98	0	14	2,933	1.21	0	14	1	0.75	100
15	88	0.98	0	15	3,562	1.21	0	15	1	0.74	100
16	86	0.98	0	16	4,310	1.21	0	16	1	0.75	100
17	84	0.98	0	17	5,226	1.21	0	17	1	0.75	100
18	82	0.97	0.1	18	6,283	1.2	0	18	1	0.75	100
19	80	0.98	0.1	19	7,614	1.21	0	19	1	0.75	100
20	78	0.97	0.7	20	9,198	1.21	0	20	1	0.75	100
21	76	0.97	0.7	21	11,037	1.2	0	21	1	0.75	100
22	74	0.98	1.5	22	13,359	1.21	0	22	1	0.75	100

Source: Table format by M. J. Bigelow.

stages: (1) seed bank, (2) seedling, (3) juvenile, (4) vegetative adult, and (5) reproductive adult. With the exception of seedlings, all stages can transition to the next stage or remain in their present stage (stasis). Reproductive adults can transition backward to vegetative adults, and are the only stage that can contribute to seed bank and seedling stages. Maschinski and her colleagues, like Sieg and King, determined transition rates by following the fates of individually marked plants in designated plots spread across four habitat patches that covered the range of the cliffrose, and from plants under observation in a greenhouse over seven "transition years," from 1996–2003 (a "transition year" is a period of time in which the transition rate was computed over 2 consecutive years, from one year to the next, for example, 1996–1997, 1997–1998, and on through 2002–2003). Separate transition matrices were developed for dry sites and for moist sites, and environmental stochasticity was added by developing different matrices for average, dry, and moist weather conditions and running separate simulations in which transition matrices were assigned either (1) randomly (equal probability for all weather conditions), (2) using actual probabilities from weather conditions over the past 100 years, (dry years = 0.104, wet years = 0.24, average years = 0.656), (3) with assumed 20% increase in aridity (dry years = 0.144, wet years = 0.14, average years = 0.716), or (4) 40% increased aridity (dry years = 0.184, wet years = 0.004, average years = 0.812), with the last two scenarios intended to simulate predicted effects of global warming.

Designed with these parameters, the PVA projected that Arizona cliffrose would decline slowly on both moist and dry sites (Figure 8.19a and b, respectively), with small

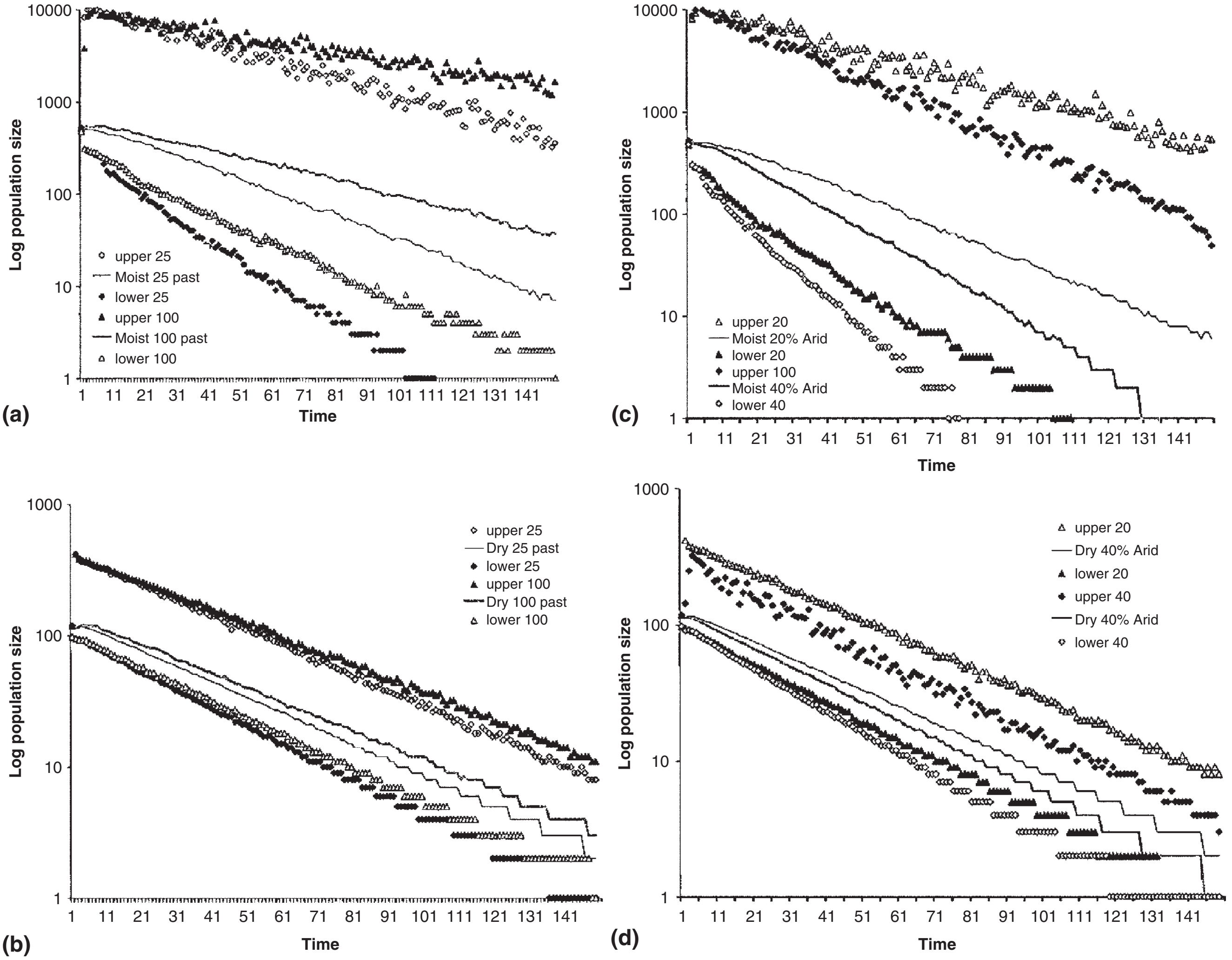

FIGURE 8.19. Projected population size of Arizona cliffrose (*Purshia subintegra*) on moist sites (a) and dry sites (b) based on population viability models generated with 1,000 simulations run for 150 years under random and 100-year past climate scenarios, compared to projected population sizes on moist sites (c) and dry sites (d) with 20% and 40% increased aridity compared to historic conditions. Upper and lower 95% confidence limits are indicated for each scenario. (Maschinski et al. 2006, Using population viability analysis to predict the effects of climate change on the extinction risk of an endangered limestone endemic shrub, Arizona cliffrose, *Conservation Biology,* Copyright 2006 by Blackwell Publishing.)

populations on both and a 20% probability of extinction on moist sites. Although no extinctions (0 individuals) were projected on dry sites, the average population size declined to <20 individuals in 150 years, a form of the "quasi-extinction" discussed earlier, a level from which the population would be unlikely to recover. When using the past 100 years of weather records for climate averages, populations declined more slowly with more years of average conditions. With increased aridity, extinction probability accelerated on moist and dry sites (Figure 8.19c and d, respectively). Within 105 years, the probability of extinction at the moist site increased to 19% for the 20% arid model and to 63% for the 40% arid model. Thus, these models suggested that patches of *P. subintegra* would shrink to extinction at varying rates under present trends of global warming. In elasticity, stasis elements for vegetative adults (the probability of remaining a vegetative adult plant from one year to the next) had the greatest effect on the value of λ (population growth), but changes in the values of the seed bank and adult fecundity (seed production) had little effect.

Given the model projections, Maschinski et al. concluded, "Our models suggest that the *P. subintegra* population in Verde Valley is slowly declining and will be at greater risk of extinction with global warming.… Because it is possible that the Verde Valley habitat may not be able to sustain larger numbers of *P. subintegra* under conditions of increased aridity, experimental attempts to introduce the species to higher moister sites are recommended. This solution is complicated by the presence of a common cogener, the Stansbury cliffrose, *P. stansburiana*, that grows at higher elevation and is known to hybridize with *P. subintegra*" (Maschinski et al. 2006:226–227).

The Arizona cliffrose study reveals some of the key advantages and disadvantages of model making and PVA applications. First, there is ***heuristic value*** in constructing the model. The PVA for the cliffrose and the western prairie fringed orchid both serve as focal points for organizing long-term monitoring data into a more precise assessment of the potential for recovery of these populations. When a PVA is stage-based, it can be used to identify particular life stages that might be most vulnerable to extinction and thus be the primary targets of management. Further, in a stage-based PVA like that of the Arizona cliffrose, the data demands require us to understand the life history of the species fully and precisely, and to design research and monitoring programs in such a way, and for a sufficient period of time, that we can estimate the actual probabilities of individuals transitioning from one life stage to another. For the cliffrose, we must estimate transition rates in different environments (dry sites vs moist sites), thus forcing us to examine populations and predict their trajectories under a variety of environmental conditions.

Second, the outcomes of the model, with elasticity analysis, reveal expected general trends and help to identify real threats to the population, as well as dismiss possible concerns that, upon analysis, prove to have no real effect. In this example, we learn that the greatest threat to population persistence is not whether the population is on a dry or moist site, but what sort of overall precipitation regime (dry, wet, or average) it encounters during the year. Likewise, the elasticity analysis tells us that any environmental change or management action that affects the transition of vegetative adults to reproductive adults greatly influences population growth; however changes in seed production or in numbers of seeds in the soil have little effect.

These insights lead to the third dimension of the model's value: the suggestion of possible management strategies with improved insight of choosing the best management option among an array of possible strategies. For example, given that seed production and availability have little effect on population growth, a management plan to reduce seed predation on the Arizona cliffrose would be a waste of time and effort. Similarly, given that populations suffer declines on both dry and moist sites, it would make little sense to transplant dry site populations to moist sites in hopes that they would do better. What would make sense, as the authors note, is to transplant individuals from their present range to one which has more years of average precipitation and fewer dry years. This strategy is likely to increase transition probabilities of vegetative adults becoming reproductive (flowering) adults, and reduce population decline and extinction risk, although it increases the risk of hybridization with a more common species, a problem of conservation genetics already examined (Chapter 6).

As the cliffrose study reveals some of the advantages of model building and PVA, it also reveals their limitations. The actual estimates of population decline and extinction risk are probably incorrect in absolute terms. Uncertainty is high (for example, on moist sites, the 40% increased aridity model produced population estimates from 0 to 10,000) (Maschinski et al. 2006), and any use of the model to make precise future population estimates of this species is almost certainly misguided. Even more limiting is the fact that the model is data demanding, and the kind of data required are long term. This means that if data are deficient and extinction is imminent, there will be no time to construct a reliable PVA and managers would be better off to take quick action, even if not fully informed.

Such demands and contingencies could prevent managers from constructing reliable PVAs, especially for endangered populations which have few individuals to monitor or manipulate. One way to overcome this limitation is through the use of "surrogate" population studies, in which a closely related common species, or a more viable population of the same species, "stands in" for the threatened species or endangered population, providing data and opportunity for monitoring and manipulation that lead to construction of a PVA with management insights valuable to preventing extinction of its endangered counterpart. For example, Schtickzelle et al. (2005) developed a PVA for endangered populations of endangered cranberry frittilary butterfly (*Boloria aquilonaris*) populations in The Netherlands from studies of larger populations in Belgium. This species is a glacial relict, restricted to peat bogs because common cranberry, *Vaccinium oxycoccus*, a peat bog endemic plant species, is the only host plant of its caterpillars. This butterfly, like the Arizona cliffrose, is threatened by global warming trends that reduce the number and extent of peat bogs and their vegetation. Based on projections of their model, Schtickzelle et al. (2005) concluded that the primary threat in The Netherlands was habitat loss. To save this species in The Netherlands, large scale restoration of habitat patches would be necessary (i.e. more and larger peat bogs would have to be established) because there are not enough of these habitats for the species to survive.

8.5. Making Management Decisions for Small Populations

8.5.1. PVA and the Analysis of Risk

It may be presumptuous to think that modeling can define a minimum viable population (Boyce 1992), but PVA can, when combined with techniques of adaptive management and risk analysis, contribute to early recognition of problems associated with small populations and provide an accurate assessment of the nature and extent of these problems. PVA models can even suggest an appropriate solution and provide standards with which to evaluate solutions to see if they are effective when implemented. PVA also offers the ability to continue evaluation of the problem over time, as well as to evaluate the effectiveness of management efforts to solve it (Lindenmayer et al. 1993).

Conservation biologist Mark Boyce (1992) advocated combining PVA with techniques of ***adaptive management*** (applying management actions in experimental ways and designs) in managing spatially disjunct populations. Such "management experiments," properly designed and effectively combined with risk assessment, could enable managers to evaluate the effectiveness of different conservation strategies (Lindenmayer et al. 1993). This synthesis of approaches and techniques is necessary because the management of any population, with or without PVA, is a problem of ***decision analysis*** (DA). For every hypothesis we form about the factor or factors that limit a small population, there is a corresponding management option appropriate to the hypothesis. For every hypothesis-management combination, there is some probability of different states of the population or its environment that might occur as a result. DA can be applied to three kinds of management decision problems. These are classification problems, ranking problems, and selection problems (Drecshler and Burgman 2004).

In classification problems, management actions are categorized into a number of discrete classes, such that different conditions in a population might lead to the same action. For example, for a game species, a management action such as "stop hunting" might be employed if the species reached a critically low threshold, or if environmental conditions during a reproductive period eliminated recruitment in a particular year.

In a ranking problem, possible management actions are given a rank order from best to worst. For example, a manager of a tallgrass prairie might consider using prescribed fire, regulated grazing, mowing, or no action as four different means of increasing the population of a rare plant species. An effective decision analysis algorithm would be able to rank such possible actions from best to worst.

The third kind of decision analysis problem is a selection problem. In this kind of problem, the analyst or manager must identify (select) a subset of "best" actions from a larger set of possible actions. If there is only one decision criterion, then the DA should produce a single "best" management action relative to this criterion. For example, suppose a manager determines that a small, forest-dwelling population of endangered animals, now consisting of 100 individuals, is most threatened by the potentially catastrophic effects of forest fire. A manager may have the choice of maintaining the endangered population as single unit at one location, which will maximize the effective population size, or of translocating half of the animals to a different site to reduce the risk that a fire could destroy the entire population. Suppose that the probability of a fire over the next 100 years is estimated at 0.10, and that the probability of extinction over this time under non-catastrophic environmental conditions for a population size of 100 is 0.05, but the probability of extinction for a group of 50 is 0.15. Which strategy minimizes the risk of extinction?

If we display our choices and their probabilities as a decision tree (Figure 8.20), we can evaluate all possible outcomes and their probabilities. If the population remains as a single unit and there is no fire, the extinction probability is 0.05. If a fire occurs, their extinction is certain ($pE = 1.0$). Their expected probability of extinction is then the sum of the probabilities of these events, or $(0.05 \times 0.9) + (0.1 \times 1) = 0.045 + 0.1 = 0.145$. If the population is managed as two units, there are four possibilities: (1) a fire occurs in both units; (2) a fire does not occur in either unit; (3) and (4) a fire occurs in one unit but not in the other. The probability of a fire in both units is $0.10 \times 0.10 = 0.01$; and the probability that a fire does not occur in either unit is $0.9 \times 0.9 = 0.81$. The probability of a fire in at least one unit but not in both is $0.1 + 0.1 = 0.2$. Therefore, the extinction probability of the two subunits is $(0.01 \times 1) + 2(0.04$

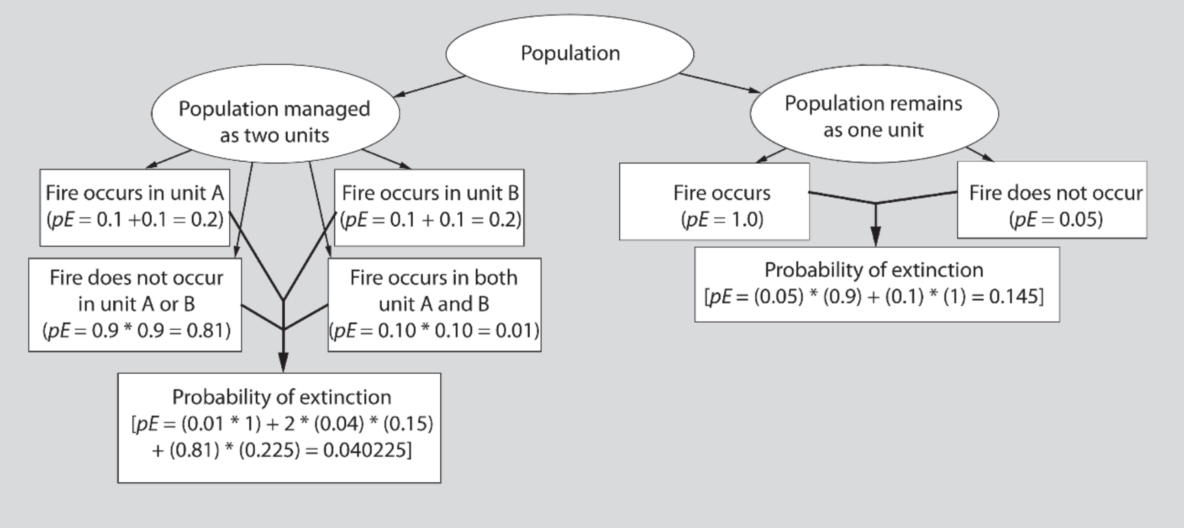

FIGURE 8.20. A decision tree of risk analysis for the probabilities of extinction for a population managed under two different management strategies. When combined with results of a population viability analysis, risk analysis can provide valuable insight into the relative risks of different management strategies for a population with given characteristics.

× 0.15) + (0.81 × 0.0225) = 0.01 + 0.012 + 0.018225 = 0.040225. In this case, extinction risk is more than three times as high for the single large population as for the separated populations. This kind of analysis has been used in the past on actual endangered species, such as the whooping crane (*Grus americana*) to determine whether it was better to manage the species as a single large population or as two smaller populations (Figure 8.21) (Maguire 1986). In this case, the greatest environmental risk was considered to be that of a severe storm striking the population, particularly on its historic wintering grounds on the Texas Gulf Coast (USA). The single decision criterion is to minimize extinction risk.

Ideally, PVA and DA would be coupled in making management decisions in conservation. Alone, DA may be obviously one dimensional. In the whooping crane decision tree, the only serious threat considered is environmental catastrophe (a violent storm), but other threats could also cause extinction in this population. PVA could be used to help identify such threats, to estimate the degree of risk (probability) associated with each threat, and the sensitivity (elasticity) of the population to each threat. Informed by a carefully constructed PVA, our DA would be more complex, but also more realistic, and our management decision would really be better management.

Even if DA and PVA are closely coupled, there are many assumptions inherent in the process. The DA assumes that the probabilities it derives from the PVA are accurate estimates of the probabilities of these events. It also assumes that catastrophes like forest fires or storms are independent events in the two areas (they may not be if the two areas are not sufficiently far apart). As already noted, using PVA to aid decision analysis for endangered species is problematic. Many kinds of critical data probably cannot be obtained because the population's small size makes direct handling or experimental manipulation an unacceptable risk. The irony is that it is often in cases of endangered species that a reliable PVA is most needed for management decisions that are most critical. Thus, far from solving all dilemmas of population management, PVA may create

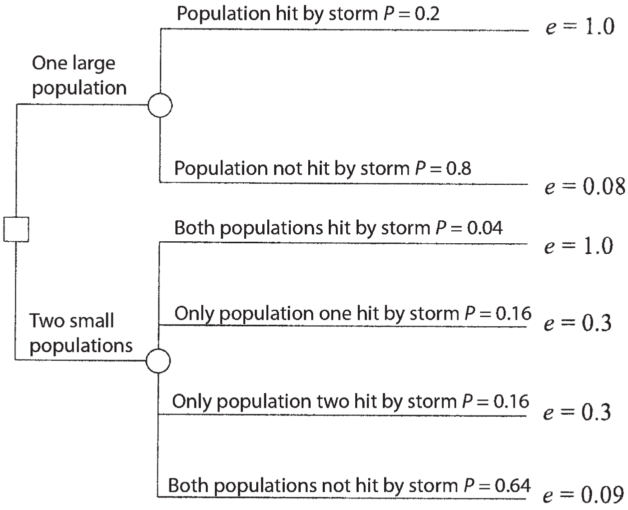

FIGURE 8.21. A decision tree representing the probabilities of extinction of different sized whooping crane (*Grus americana*) populations under different management scenarios relative to the risk of potential elimination by severe storms. (Drechsler and Burgman 2004. Copyright 2004, Springer-Verlag, New York, Inc. With the kind permission of Springer Science and Business Media.)

some of its own. These limitations are not reasons to avoid using PVA, but rather constraints to be appreciated so that its results are not misunderstood or misapplied in the course of the decision analysis that follows.

8.5.2. The Problem of PVA Application: How Do We Use and Interpret Population Viability Analyses?

PVA can be used to improve many aspects of conservation policy. PVA permits the problems associated with small populations to be defined in greater detail and may facilitate selection of a more appropriate response to those problems than could be made through other means of analysis. PVA also can lead to better appraisal of management efforts (i.e., did the policies and management strategies employed solve the problem?).

Like all models, PVA forces conservation biologists to make explicit what is known about the population, as well as current assumptions about unknown population parameters. PVA serves a purpose in assembling known facts in a meaningful way, while also identifying areas of research needed to make such analysis more reliable or information needed for management planning (Lindenmayer et al. 1993). PVA can synthesize interacting factors and identify trends in population behavior and it can identify processes that threaten the population. It can even be used in defining the "minimum critical area" for a species, a valuable concept in designing reserves.

PVA is often used in a single-species approach to conservation, which is understandable because a PVA's unit of interest is a population, not a community. In a strict sense, this limitation is less a criticism of the method than of the lack of PVA-equivalent techniques for larger biological units. It would be a poor carpenter that criticized his saw because it cut wood well but performed poorly in driving nails. It is important to recognize that PVA was developed for and should be used primarily on a population-by-population basis. It is not an appropriate technique for evaluating the viability of communities or ecosystems, nor is it equally well suited to all *types* of populations. This limitation is being removed as a greater and more diverse array of PVA analysis programs are being developed, although even more recent reviews of PVA applications still show a preponderance of PVAs applied to birds and mammals (74%) (Henle et al. 2004). Overall, PVA simplifies the dynamics of populations as well as interactions among different environmental and demographic parameters. Such simplification reduces the correspondence between the model and the real population. Acknowledging this limitation helps to identify specific areas in which models for PVA can be improved and their correspondence to real populations increased.

Other serious criticisms of PVA have arisen from rigorous mathematical analysis of its inputs and outputs. Mathematician Donald Ludwig calculated quasi-extinction probabilities of natural populations from time series of census data of estimated abundance in several different animal populations (Ludwig 1999). Even when errors in estimates were ignored, confidence intervals associated with extinction probabilities were large. In three species of birds, the Laysan Finch (*Telespiza cantans*), Palila (*Loxiodes baillieu*) and Snow Goose (*Chen caerulescens careulescens*), most confidence intervals included extinction probabilities of 0 and 1, rendering them meaningless. When errors in estimates were included, things got worse. Ludwig demonstrated that neglecting observational errors produced a bias in the extinction probability that significantly lowered its value, thus giving an overly optimistic estimate of the probability of population persistence (Ludwig 1999). Ludwig concluded "A proper population viability analysis should include estimates of likely ranges in parameter estimates based upon available data and also include the corresponding ranges for quantities related to extinction. The results should not be regarded as reliable unless the ranges are small. In view of the difficulties cited above, it is difficult to imagine reliable estimates of small extinction probabilities for populations that appear to be threatened" (Ludwig 1999).

8.5.3. Can PVAs Predict the Future? Test Cases and General Trends

In most cases it is not possible to estimate population viability empirically. PVA is usually applied to rare or threatened species whose small numbers often preclude more empirical studies that might tell us if results expected from a model agree with results observed in the field. But sometimes it is possible to make this comparison, and it can be particularly useful to do so. Australian conservation biologists Stephen Ball, David Lindenmayer, and Hugh Possingham used ALEX (Analysis of the Likelihood of EXtinction) software to predict probability of patch occupancy for two species of small native Australian mammals, the bush rat (*Rattus fuscipes*) and the agile antechinus (*Antechinus agilis*) (Ball et al. 2003). These mammals are not endangered, but both prefer riparian habitat that is being increasingly fragmented in the Australian landscape. For each species, Ball and his colleagues considered different scenarios of dispersal between patches (none or 25%), the level of environmental stochasticity (variability) (high or low, based on standard deviations from average habitat quality values in each year, SD = 0.50 and SD = 0.25) and amount of suitable habitat, based on stream width (25 or 40 m), creating a total of eight scenarios. ALEX retrospectively predicted patch occupancy of each species for each scenario from 1900 to 1997. In 1997, observed patch occupancy was determined from field trapping, although this data was not used in the model.

None of the scenarios of predicted patch occupancy were good matches for *Antechinus agilis* and only one for *Rattus fuscipes* (low environmental variation, zero dispersal and 40 m stream width, representing large habitat patches). All scenarios consistently underestimated patch occupancy for both species, although there was a consistently positive relationship between the model's probability estimate of patch occupancy and actual patch occupancy, indicating that the model was making predictions "in the right direction" (Ball et al. 2003), even though the predictions were inaccurate.

In a similar test, Lindenmayer et al. (2001) compared the ALEX-generated predictions of patch occupancy in a fragmented Eucalyptus forest for another Australian mammal, the greater glider (*Petauroides volans*) with actual patch occupancy determined from field surveys. In this case, the greater glider was treated as a metapopulation and modeled in four different scenarios that varied in habitat quality (uniform vs patch specific) and immigration (none vs animals moving into patches from surrounding forests). In this case, all four scenarios shows significant positive correlations between predicted and observed patch occupancy (Figure 8.22).

These examples address the reliability of PVA with individual models designed for particular species. Conservation biologists Michael McCarthy, Sandy Adelman, and Hugh Possingham took the idea of testing the reliability of PVA a step further by evaluating the reliability of predictions made by models in both absolute and relative terms over a much larger array of conditions (McCarthy et al. 2003). Using a stochastic Ricker model (a model originally developed in fisheries research that predicts changes in population recruitment based on changes in the number of adults, or "stock" of a population) to generate actual population data for 10, 20, 50, or 100 years, McCarthy and his colleagues created 160 simulated "species" to be evaluated, each with different life history characteristics and, therefore, different model parameters in rates of birth, death, age structure, breeding systems, migration patterns, and other demographic variables (McCarthy et al. 2003). For each unique parameter combination (species), they compared the predicted risks of extinction calculated by the model to the "true" risk of extinction via stochastic simulation of the original model for 1,000 iterations. Like Ludwig, they found that PVA estimation carried a high level of uncertainty, and inaccuracy, in estimating the true risk to extinction. However, McCarthy et al. also asked three additional questions. First, could PVA accurately assess the relative changes in risk factors to a population over time? That is, could it identify which factors were more important to population viability than others over a specified period of 10–100 years? Second, could PVA accurately rank two or more species in *relative* extinction risks? That is, do PVAs accurately identify which species is at the *most* risk in an array of modeled species? Third, could PVA accurately identify the better of two management options that would decrease the overall risk of extinction to a given species, even if it could not predict the exact probability of extinction with accuracy?

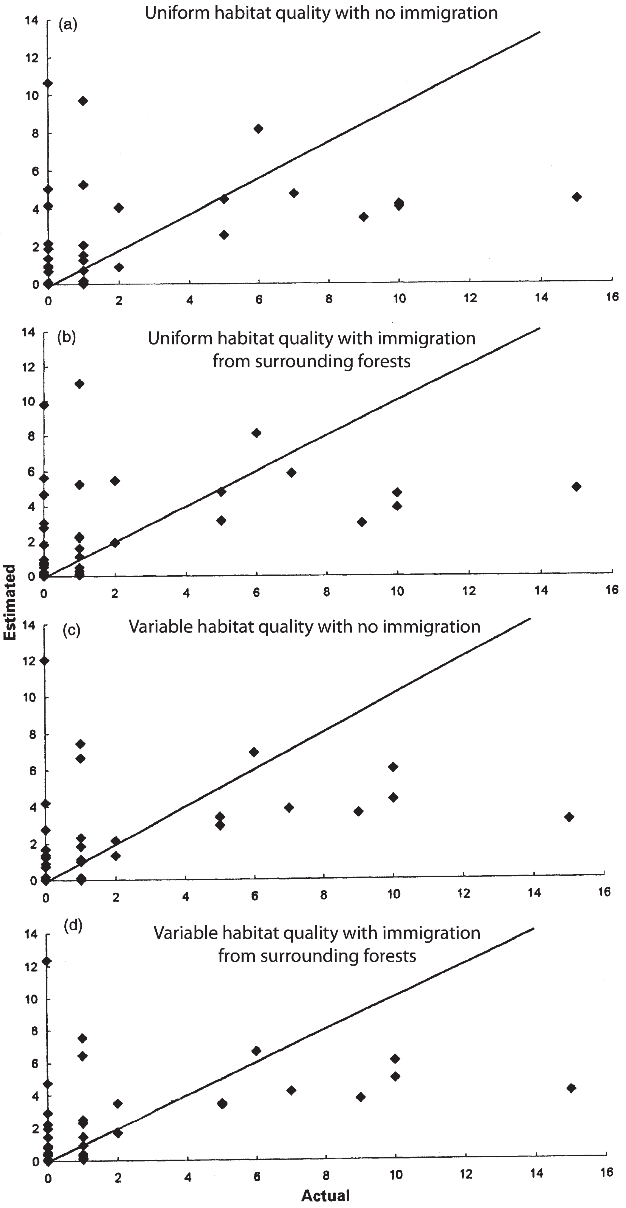

FIGURE 8.22. Relationship between actual and estimated abundance of the greater glider (*Petauroides volans*) in fragmented Eucalyptus forests in Australia under four scenarios of varying habitat quality and immigration. All scenarios show significant ($P = 0.001$–0.006) positive relationships between actual and estimated abundance under assumptions of logistic regression. (Lindenmeyer et al. A landscape-scale test of the predictive ability of a spatially explicit model for population viability analysis, *Journal of Applied Ecology,* Copyright 2001 by Blackwell Publishing.)

In relative assessments, all three questions were answered affirmatively. McCarthy et al. found that PVA was highly reliable in *ranking* alternative risk factors to population persistence in a given species and could reliably rank which species were more at risk of extinction than others.

Specifically, the rank (Spearman) correlations between predicted risk and actual risk of extinction for all 160 simulated "species" was 0.59 even with only 10 years of data (in other words, 59% of the variation in ranks in actual species' extinction probabilities could be explained by variation in the predicted rank in species extinction probability) and 0.89 with 100 years of data. Consideration of PVA results also led to choosing the correct management strategy 74% of the time with 10 years of data and 92% of the time with 100 years of data (McCarthy et al. 2003).

Based on their assessment, McCarthy and his colleagues concluded that, although PVA cannot necessarily provide accurate estimates of absolute extinction probability, it is a valuable decision-support tool in population management, especially of threatened species, because it can accurately rank relative threats and can usually help identify the superior management strategy to address such threats. In doing so, PVA can, when compared among different species, be an aid to determining which species might need most urgent attention and management. McCarthy et al. also noted other advantages of using PVA. "Population viability analysis can use more data, the level of detail in the model is flexible so that an appropriate level of complexity can be chosen, and there is an explicit relationship between the parameters of the model and the fate of the population. An additional advantage of PVA over alternatives for classifying the conservation status of species is that the population models can be used to improve management strategies" (McCarthy et al. 2003:988).

8.5.4. A Final Review: What Are We to Think of PVA?

To paraphrase population modelers Ken Burnham and David Anderson; models never tell the truth, they are just the best possible approximation of it (Burnham and Anderson 1998). As a model, PVA is a description of demographic and environmental stochasticity projected into the future. Like all models, constructing a PVA forces us to make our assumptions explicit and to identify the processes and parameters that influence our conclusions. But this is an advantage of model building, not model output. PVA can help managers make more informed judgments, but neither its assumptions nor its predictions can be empirically tested. PVA is expected to be defensible against legal challenges, but given its uncertainties, it may not be able to withstand them. Thus, biologists who perform PVA may fail to meet the expectations of their employers (Ludwig 1999), particularly if the employer is a government agency whose decisions are accountable to the public and potential targets for litigation.

Unfortunately many conservation biologists forget the limitations of PVA and incorrectly use it as a diagnostic tool to determine why populations are declining and how to save them from extinction. PVA has no power to diagnose the causes of decline or prescribe a remedy for it, but PVA may provide, when combined with human discernment, clues that lead the investigator to correctly identify which factors pose the greatest risk to the population's persistence. PVA does not identify what made the population small in the first place or what must be done to make it bigger. Neither has PVA, so far, been able to accurately predict extinction. In an extensive review of PVAs associated with endangered species, Mark Shaffer and his colleagues noted that "We can find no example of a PVA that has been used to forecast the extinction of a wild population that actually happened within the confidence limits of the model …" (Shaffer et al. 2002:127). Again to quote McCarthy et al., "Although the results of our study suggest that PVA can assist such decisions even when the predictions remain uncertain, PVA predictions should be assessed with field data so that the models (and therefore the decisions based on them) can be improved further. The process of parameter estimation, model construction, prediction, and assessment should be viewed as a cycle rather than a one-way street" (McCarthy et al. 2003:987). Three things affect the quality of any PVA and the reliability of its results: (1) the quality of model's data and appropriateness of its structure to the population(s) studied; (2) the level of uncertainty associated with the model's results; and (3) the quality of review the model was subject to prior to its final form and publication (Reed et al. 2002). The model's results are predictions, not observed events. Therefore, one of their most appropriate uses in research is to be used as hypotheses to be tested in actual experiments in field and captive populations.

The key to a population's recovery is not simply an analysis of existing conditions, but a correct diagnosis of the problem and the wisdom to achieve a successful solution (Caughley and Gunn 1996). Similarly, PVA cannot be presented in public, in court, or in scientific journals as an estimate of certainty. Its level of uncertainty may be large, even unacceptably so. Again Ludwig addresses the issue perceptively, "… an exaggeration of our capabilities carries a high risk of failure and subsequent disillusionment. It would be better to be more modest about our understanding and achievements, and to help decision makers understand the complex, realistic arguments that pertain to most conservation decisions" (Ludwig 1999).

8.6. Synthesis

Conservation biology has rightly sought to distance itself from the *single species management* approaches that characterized applied resource management sciences in the past, an approach that led to entire communities and ecosystems being managed for the benefit of one or a few species. However, conservation biology must not confuse single species management with *species specific conservation*, an approach that should be valued and practiced if conservation biologists hope to see the recovery of threatened and endangered populations. Populations are the primary currency and concern of conservation biology, and the need remains to define populations more rigorously in order to avoid misunderstanding and mismanagement. This is particularly critical at a time when more and more populations are threatened with extinction, and when many species have been reduced to only scattered disjunct populations with few individuals.

Conservation biologists must mature in their recognition of PVA as an analytical technique rather than a diagnostic tool, and thus better appreciate its limitations. The estimate of population persistence and "extinction thresholds" should not be made solely through PVA, but should include a detailed assessment of the ecology of the species at risk, and conservation biologists should incorporate risk analysis and adaptive management procedures into assessments of PVA before determining final management strategies to restore small populations to viable numbers.

The dreadful urgency of attempting to save many small and declining populations from imminent extinction compels conservation biologists to implement management strategies quickly. However, this combination of concern and rapid response must not tempt conservation biologists to be careless in their systematic analysis of the causes of a population's decline. Each assessment of cause must be framed as a carefully constructed hypothesis that leads to specific predictions, a clear and practical management strategy, and measurable way to test consequences that determine its veracity.

Appendix: Calculation of Columns in a Cohort Life Table

x Column

Age is presented as an interval ($x - x'$), typically in years.

nx and dx columns

dx is the number dispersing or dying in each interval. By knowing this number, and the initial number of individuals in the cohort (N), we can calculate the number surviving to the beginning of the next age interrval (n_x).

$N - d_x = n_x$ for the second age interval

$n_x - d_x = n_x$ for each subsequent age interval

l_x column

Survivorship (l_x) is equal to the proportion of the original cohort surviving to the *beginning* of each age interval. By definition, survivorship is 1 for the original cohort and goes to 0 during the life span of the longest-lived individuals in the cohort.

$n_x = l_x N$

q_x column

The age-specific disappearance rate (q_x) is the proportion of the population that dies or disperses during a particular age interval.

$d_x = q_x N$

e_x column

e_x is the future life expectancy, usually expressed in years. To calculate life expectancy, two additional statistics are necessary: L_x and T_x. L_x is the average time units lived by all individuals in each category within the population. L_x is found by summing the number alive at age interval x and the number at age $x + 1$, and dividing the sum by 2. T_x is the number of time units left for all individuals to live from age x onward. To calculate T_x simply sum all of the values for L_x from the last age interval up the column until the age interval of interest. e_x is then calculated by dividing T_x for the particular age class x by the survivious for that age, as given in the n_x column.

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9

Population Management and Restoration

The extinction process has little to do with the death rattle of the final actor. The curtain in the last act is but a punctuation mark – it is not interesting in itself. What biologists want to know is about the process of decline in range and numbers.

Michael Soulé 1983:112

In this chapter, you will learn:

1. **How to estimate a population's probability of persistence and initiate investigations to determine that probability in specific populations**
2. **How to develop a plan for the conservation of a small and declining population and experimentally identify the factors most important to its recovery**
3. **What are the social, political, and legal conditions that support population restoration**
4. **Why non-native species pose a threat to native populations and how such threats can be controlled**

9.1. Minimum Viable Populations and Recovery Strategies for Threatened Species

9.1.1. General Considerations

In Chapter 8 we saw how models offering a Population Viability Analysis (PVA) could be constructed, what kinds of analyses they might be able to perform, and how they might be applied to real populations. In this chapter, we continue our investigation of population conservation by examining specific case histories of conservation management in small populations, as well as examining the management of populations of non-native species, populations that we often *want* to remain small, or even eradicate altogether.

We have noted earlier that genetic considerations were the original source of estimates of minimum viable populations in conservation biology, beginning with Franklin's (1980) suggestion that effective population sizes of 50 were needed to prevent deleterious effects of inbreeding, and a minimum effective size of 500 was required to maintain sufficient genetic variation to be able to respond to continuing environmental variation. We also have noted that such "rules" were too general to be of value to specific populations. In many cases, much larger numbers may be required. Of greater importance is the fact that such an estimate of MVP reflects only genetic considerations. Modern population viability analysis considers demographic, environmental, and genetic characteristics of a population, and shifts its emphasis from focusing on the minimum size needed for a viable population (MVP) to more complex and comprehensive estimates of the probability of the population's persistence through time under different environmental, demographic, and genetic scenarios.

There are five main avenues for conducting an effective investigation of a population's demography and determining its probability of persistence through time. These are: experiments, biogeographic patterns, theoretical models, genetic considerations, and simulation models. Not all are equally useful, practical, or precise in estimating persistence probabilities, especially for small populations. Experiments are often inappropriate, not to mention risky, to conduct on small populations to determine how small they can become before extinction occurs; the outcome of such an experiment could well be another extinct species. The second approach, an examination of biogeographic patterns of disjunct populations of a species over a large area, does provide some first-order approximation of the minimum sizes of areas that populations can use, and the (apparent) minimum number of individuals that sustainable populations must have. However, as in all descriptively oriented data, the inferences drawn may be unreliable. Various factors, all uncontrolled in a simple examination of the biogeographic pattern, may affect the population and area sizes used by species because population characteristics vary widely in different areas and habitats. Populations with minimum numbers and minimum areas may not be stable populations. They may, in fact, be already declining to extinction. Thus, the use of a minimum for decision rules in management and conservation could doom a population. A biogeographic approach will not provide worthwhile results unless information is available on dispersal, migration, and colonization rates of new habitats. And, perhaps most obviously, a biogeographic approach will not work well with species that do not inhabit sufficiently large areas or that do not inhabit insular or patchy habitats.

A third approach, theoretical models, have been employed in some cases to determine the probability of population persistence. One such model is diffusion theory, in which the movement, dispersion, and growth of a population are assumed to follow the principles of diffusion observed at a molecular level. However, most organisms do not behave precisely like molecules of gas, and the theory requires environments completely unpredictable to the organism for its assumptions to be valid. Many other models, although elegant in their simplicity, also contain unrealistic assumptions or unresolved mathematical difficulties (Shaffer 1981). Because every species is unique, general theoretical models often fail to achieve realism when applied to the particulars of individual species' demography.

Despite the difficulties in these approaches and those associated with the remaining options of genetic considerations and simulation models, conservation biologists must do the best they can with available knowledge and techniques, and there is especial urgency to their efforts for populations that are already small and getting smaller. To understand how such probability can be estimated through an integrated analysis of population processes, and applied to understand the dynamics of declining populations, we take up the case history of an endangered European bird species, the Little bustard (*Tetrax tetrax*).

9.1.2. The Use of PVA to Identify Threats and Recovery Strategies in *In Situ* Populations: The Case of the Little Bustard

The Little bustard (Figure 9.1) was once a common bird found across much of Europe and Asia, where it lives in grassland-steppe environments. Like the sage grouse and prairie chicken of North America, male bustards gather on special breeding grounds or "leks" in spring where they display to observing females with elaborate physical movements or "dances." During the last century, the Little bustard has suffered declines throughout its range, primarily from increased cultivation of its grassland habitat and from more intensive agriculture use in areas already

FIGURE 9.1. The Little bustard (*Tetrax tetrax*), once a common bird of European grasslands, is today declining throughout its range. (Photo courtesy of Gérard Schmitt.)

cultivated. Increased cultivation destroys bustard habitat, and more intensive agriculture, through increasingly high levels of pesticide applications, destroys arthropods, one of its most important food sources, especially for chicks up to the fledgling stage. The decline has been particularly severe in France. From an already reduced population of 7,200–8,500 breeding males in 1978–1979, further declines saw the French population plummet to only 1,300 breeding males by 2000. With associated range reduction, the number of breeding males in France's intensively cultivated central plains has fallen 90% during the same period, from 7,800 to 70 (Morales et al. 2005).

Conservation biologists Manuel Morales and his colleagues employed Vortex 7.0, a widely used model in population viability analysis, and their own field data to estimate the survival probabilities of seven endangered Little bustard populations in central-western France (Morales et al. 2005). In parameterizing the model, they provided nine foundational demographic assumptions: (1) there was no inbreeding depression; (2) the mating system was polygynous (one male mates with many females); (3) females make their first reproductive attempt at year 1, males at year 2; (4) average bustard lifespan is 10 years; (5) sex ratio at hatching is 1:1; (6) maximum number of hatchlings is 4; (7) reproduction is not density dependent; (8) individuals migrate between populations from year 1 onward; and (9) females are the migrating sex. Under these assumptions, they ran model simulations 100 times over 20 years.

Morales et al. found that population viability was most sensitive to changes in four parameters: adult survival rate, productivity per female, initial population size, and carrying capacity (Figure 9.2). Although sex ratio did not strongly affect population viability at moderate values, changes in sex ratio increased the probability of extinction if it fell below 0.3 (less than 30% males) or above 0.5 (more than 50% males). Migration also affected expected population persistence. When the model was told to assume no mortality associated with migration, the probability of population survivorship remained near 1. When mortality during migration was assumed and included in the model (a more realistic scenario), the probability of the survivorship of all population units (the metapopulation) declined to 0.9 (Morales et al. 2005).

Based on their analyses, Morales et al. noted that "In spite of high sensitivity of population survival to productivity and adult survival considered independently, the joint analysis of those two parameters in relation to population viability shows that both must reach intermediate – high values to produce a significant increase in the population's probabilities to survive. In other words, only high values of one parameter will compensate the effect of low values in the other" (Morales et al. 2005:3147). Thus, the authors concluded, "…conservation measures based on increasing productivity for the species are appropriate, although the aim would be achieved through habitat management measures guaranteeing both the non-destruction of clutches and hatchlings during agricultural labors and a significant increase of arthropod supply for chicks. The analyses also suggest that such a strategy would be appropriate for all remaining populations, despite their differences in initial population size.… Consequently, management measures addressed at improving productivity, such as promoting agricultural practices than minimize nest losses and favor insect availability for chicks (e.g. fallow and field border maintenance, reduction of pesticide input) should be a priority in the conservation strategy of these Little bustard populations (Morales et al. 2005:3148).

As this case history of the Little bustard demonstrates, managing real populations is rarely as simple as identifying a single cause of decline, eradicating one exotic competitor, or forming a hypothesis based on correlations between environmental and demographic variables. Population decline is a complex problem that may require management of multiple threats over long time spans. To better appreciate the complexity of such threats and how they can be managed, even under adverse conditions, we consider two more case histories of small and declining populations.

9.1.3. The Case History of Viper's Grass: When Large Populations Are Not Enough

Viper's grass (*Scorzonera humilis*) is a long-lived, herbaceous perennial aster, characteristic of wet, nutrient-poor grasslands and wet heathlands throughout Europe. *S. humilis* was once a common plant, but has declined in recent decades and is now endangered in many parts of its former range. The causes of its endangerment include the use of fertilizers, drainage, and land reclamation, all of which transform its preferred habitat into non-habitat, and the lack of suitable management in nature reserves. Guy Colling and Diethart Matthies developed a model of population dynamics in this species by studying five populations in southern Luxembourg (Colling and Matthies 2006). Two populations were in traditional habitat of nutrient-poor, wet grasslands. Three populations were in wet grasslands that had been regularly fertilized in the past (nutrient-rich sites). Today, all five populations are in areas of intense agricultural use and, although their sites are not fertilized, they are mown in mid-June each year. *S. humilis* reproduces and spreads through both vegetative and reproductive means. A single plant (gamet) may produce up to 100 rosettes all connected to a single large taproot. Like Sieg and King (1995) with the western prairie fringed orchid and Maschinski et al. (2006) for the Arizona cliffrose, Colling and Matthies tracked the fates of individual gamets for 4 years and rosettes for 3 years to develop a stage-structured population model that incorporated both nutrient-rich and nutrient-poor sites. Individual gamets of *S. humilis* vary in size according to growing conditions.

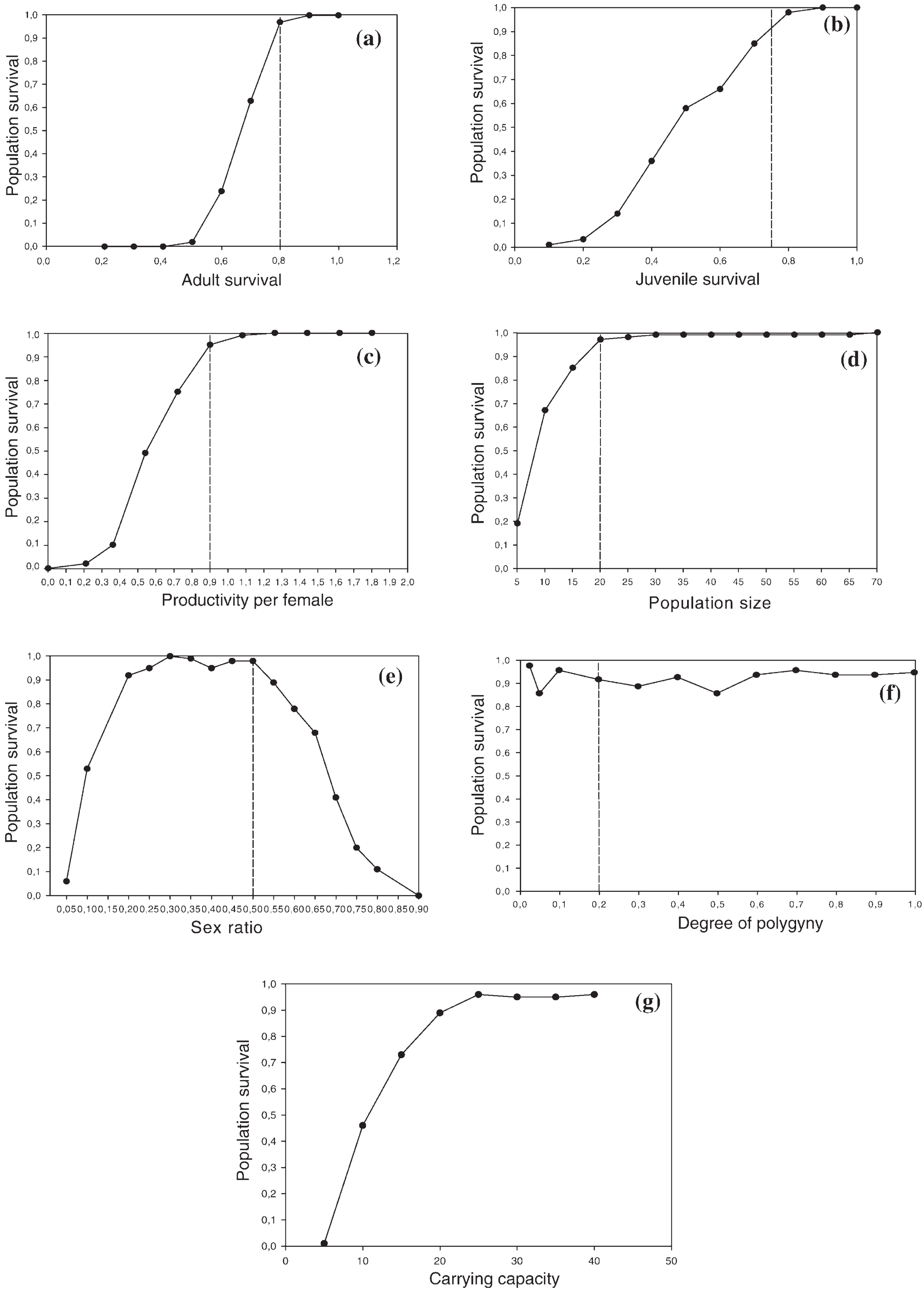

FIGURE 9.2. Sensitivity of population survival to the different parameters considered in a hypothetical Little bustard (*Tetrax tetrax*) population of 20 individuals. (a) adult survival; (b) juvenile survival; (c) productivity per female; (d) initial population size; (e) sex ratio; (f) degree of polygyny; and (g) carrying capacity. Dashed vertical lines indicate threshold values for which population survival is 0.9. (Morales et al. 2005. Copyright 2005, Springer-Verlag, New York, Inc. With the kind permission of Springer Science and Business Media.)

Thus, size does not necessarily correlate with the plant's age. Knowing this, Colling and Matthies used size to categorize individual gamets as "tiny," "small," "medium," and "large," and then determined life expectancy and survivorship based on the number of plants in each category that survived to the next year (Colling and Matthies 2006). To simulate effects of agriculture, they set up replicate blocks of plants in which each block received one of six combinations of two cutting regimes (late cutting or early and late cutting) and one of three fertilizer treatments (no fertilizer, N-fertilization, or NPK-fertilization).

Demographic data revealed that life expectancy of plants at nutrient-poor sites was greater than plants at nutrient-rich sites, regardless of size. This was true for tiny plants (16 years vs 3 years), small plants (36 years vs 16 years) and medium-sized plants (46 years vs 2 years). The life expectancy of large plants at nutrient rich sites was 20 years. At nutrient-poor sites, life expectancy of large plants could not be calculated, because all large plants survived over the 4 years of the study period, but was probably also higher than the nutrient rich site. The data suggested that the total life span of *S. humilis* may be very high, because at nutrient-poor sites yearlings need on average 15 years to reach the medium-sized stage and 30 years to reach the large stage. However, because there was no recruitment, the minimum age of plants in the different stages could not be calculated at nutrient-rich sites.

Unlike the western prairie fringed orchid or the Arizona cliffrose, there was usually little transition from one life stage to another. Not surprisingly, then, the demographic variable that most affected population growth was not a transition rate variable, but rather the rate of survival without change of stage (stasis survival rate). In contrast, changes in the rate of transition from vegetative to reproductive stages had little effect on population growth in the model. Although demographics of *S. humilis* varied little over time, dynamics at nutrient-rich and nutrient-poor sites were very different. Plants at nutrient-rich sites were old and large, but they had zero recruitment (no germination of new individuals) and higher rates of mortality compared to nutrient-poor sites, suggesting that the individuals that were present had been established at some past time when conditions on the site were different. Thus, the value of λ for populations on nutrient-rich sites was <1, indicating that such populations would decline through time. At nutrient-poor sites, λ was >1. But, despite increased recruitment, populations at nutrient-poor sites were small. All populations were affected by agricultural activities. Populations that suffered both early and late cuttings quickly declined to extinction, regardless of fertilization treatment, and a combination of late-cutting with NPK-fertilization also resulted in low survival. Although *S. humilis* is a rosette plant (basal leaves around a central axis), early mowing still removes most of the rosette because, in dense grassland vegetation, the basal leaves tend to grow vertically.

The differing responses and conditions at nutrient-poor and nutrient-rich sites in this species makes the analysis of its endangerment more complex, but a study of the model results brings valuable insights. At nutrient-rich sites, patterns are characteristic of what is known as "remnant-population dynamics." As Colling and Matthies put it, these "large populations could still persist for a long time because established plants are long-lived and relatively resistant against adverse environmental conditions." However, "the long-term prospects of these populations are poor because high productivity prevents seedling establishment and negatively affects the survival of established plants. It may take some time before productivity levels decrease to levels that allow recruitment …" (Colling and Matthies 2006:969). In contrast, "The stochastic simulations showed that the extinction risk for medium-sized populations at nutrient-poor sites is very low, but that small populations are highly threatened. Most populations in the study area are smaller than the estimated MVP of 207 individuals …" (Colling and Matthies 2006:969).

S. humilis is in a double-bind. Its large populations lack recruitment, and its small populations, which have high recruitment, risk extinction via demographic stochasticity. Thus, Colling and Matthies conclude that "most of the remnant populations of *S. humilis* are strongly threatened … [and] it may take a long time before habitat changes caused by the intensification of agriculture cease to have negative effects on the population dynamics of plants of nutrient-poor grasslands" (Colling and Matthies 2006:970–971).

The work of Collings and Matthies reveals that large population size, such as is characteristic of *S. humilis* on nutrient-rich sites, may not be an indicator of a healthy population. We can see in these results that the "ghosts of environmental conditions past" may be a primary determinant of present population status. We also see that the effects of current conditions, such as nutrient-enrichment on formerly nutrient-poor sites favored by *S. humilis*, may take years to erase. Further, the model reveals that even when habitat conditions are favorable, as on nutrient-poor sites, populations may be at risk if they are small and their habitat is limited. Thus, we begin to understand that unless humans change their methods of using land, in this case, of managing agricultural lands with high fertilizer inputs and frequent mowings, native plants cannot coexist under such "management." Finally, we perceive, as with the Arizona cliffrose, that only thorough study of an endangered population in all the environmental conditions in which it occurs gives us a true picture of the population's status and the reasons for its decline. And, even then, that picture may be complex and difficult to discern.

As we saw in Chapter 8, PVA is a data-demanding technique. It may take years to achieve sufficient information to construct a reliable model. What can conservationists do when extinction is imminent and there is no time for long term investigations? In our next case history, we see how professional insight, quick action, and a little bit of luck saved a population from extermination and put it on the road to recovery.

9.1.4. The Lord Howe Island Woodhen: A Case Study in Managing Multiple Threats to a Small and Declining Population

The Lord Howe Island woodhen (*Tricholimnas sylvestris*) (Figure 9.3) was not described scientifically until 1869 (Sclater 1869), but had been noted by European explorers visiting Lord Howe Island in the late eighteenth century. The earliest accounts describe it as an inquisitive and rather fearless bird that would often approach human visitors; indeed, biologists conducting a more recent investigation of the Lord Howe Island woodhen described it as "suicidally inquisitive" (Miller and Mullette 1985). Combined pressures of hunting, habitat destruction, and the spread of introduced feral pigs on the island caused drastic reductions in woodhen numbers and range. Pigs were the significant problem, as they destroyed ground cover in preferred habitat and preyed on nests, young birds, and adults.

By 1978, the woodhens had been reduced to ten breeding pairs located on remote areas of the island's highest mountain. By 1980, only three breeding pairs remained. Circumstantial evidence suggested that pigs were the limiting factor, even though the ranges of pigs and woodhens did not overlap, but often abutted one another. As investigators noted, "In several places, the distributions were separated only by a low rock face" that the pigs could not climb (Miller and Mullette 1985).

FIGURE 9.3. The Lord Howe Island woodhen (*Tricholimnas sylvestris*), a flightless rail found only on Lord Howe Island between Australia and New Zealand. The woodhen was nearly exterminated through a combination of hunting, habitat destruction, and predation by introduced feral pigs. An aggressive management program of woodhen protection, pig eradication, and release of captive-bred individuals to new locations has increased numbers and improved long-term prospects for the persistence of the woodhen population. Photo courtesy of John Game.

Using the evidence of the geographic distribution of pigs and woodhens as support for the hypothesis that pigs were the primary factor limiting range expansion, the Australian government began a pig eradication program in 1979 and a woodhen captive-breeding and reintroduction program in 1980. Because it was believed that current woodhen distribution was indicative of its preferred habitats, captive-reared woodhens were released on mountainous slopes at lower elevations. Although they survived and established territories, recovery was slow. A more serendipitous event provided the insight that would prove critical to the woodhen's recovery.

In 1979, a male woodhen appeared in a lowland area near the southern tip of Lord Howe Island. He defended a territory that included a large outdoor garden of the King family, long-term residents of Lord Howe Island. Soon known as the "King Garden Woodhen," the male accepted a captive-bred female released into his territory in 1981. Now "adopted" by the King family and given protection and some supplemental food, the pair laid their first clutch of eggs in 1982, but successfully raised only one chick. However, more clutches followed in quick succession, and parenting skills began to improve with experience. By the end of the year, the pair had laid nine clutches and raised 15 chicks in 11 months, plus two chicks that were raised in captivity! Biologist P. J. Fullagar, who observed the process firsthand, gained new insights on woodhen family behavior, noting that "Multiple broods were observed in which young birds from one brood assisted in defense and feeding of a subsequent brood" (Fullagar 1985). Supplemented with additional birds from the captive-breeding program (and the additional food provided by the King family), this colony of woodhens prospered to the extent that birds established territories throughout the southern end of Lord Howe Island in lowland habitats. Their increase was so rapid that within 2 years "it was becoming difficult to obtain accurate figures on their numbers" (Fullagar 1985). Up to 20 pairs were thought to be present, exceeding the numbers of the original wild mountain population. Continued growth of the King colony, successful reintroduction of captive-raised birds into other areas, and the growth of the mountain population (now unconstrained by pigs) brought the woodhen population to over 200 individuals by 1984 (Fullagar 1985). The population stabilized at around 200 individuals through 2000, but suffered a decline in 2001 to 117 individuals. Further monitoring is being carried out to determine if numbers are stabilizing at this point and to understand the cause of the decline (New South Wales National Parks and Wildlife Service 2004, www.nationalparks.nsw.gov.au/npws.nsf/Content/The + Lord + Howe + Island + woodhen).

The Lord Howe Island woodhen illustrates the key components needed for rehabilitation of a small population (Figure 9.4). First, evaluating the distribution of the

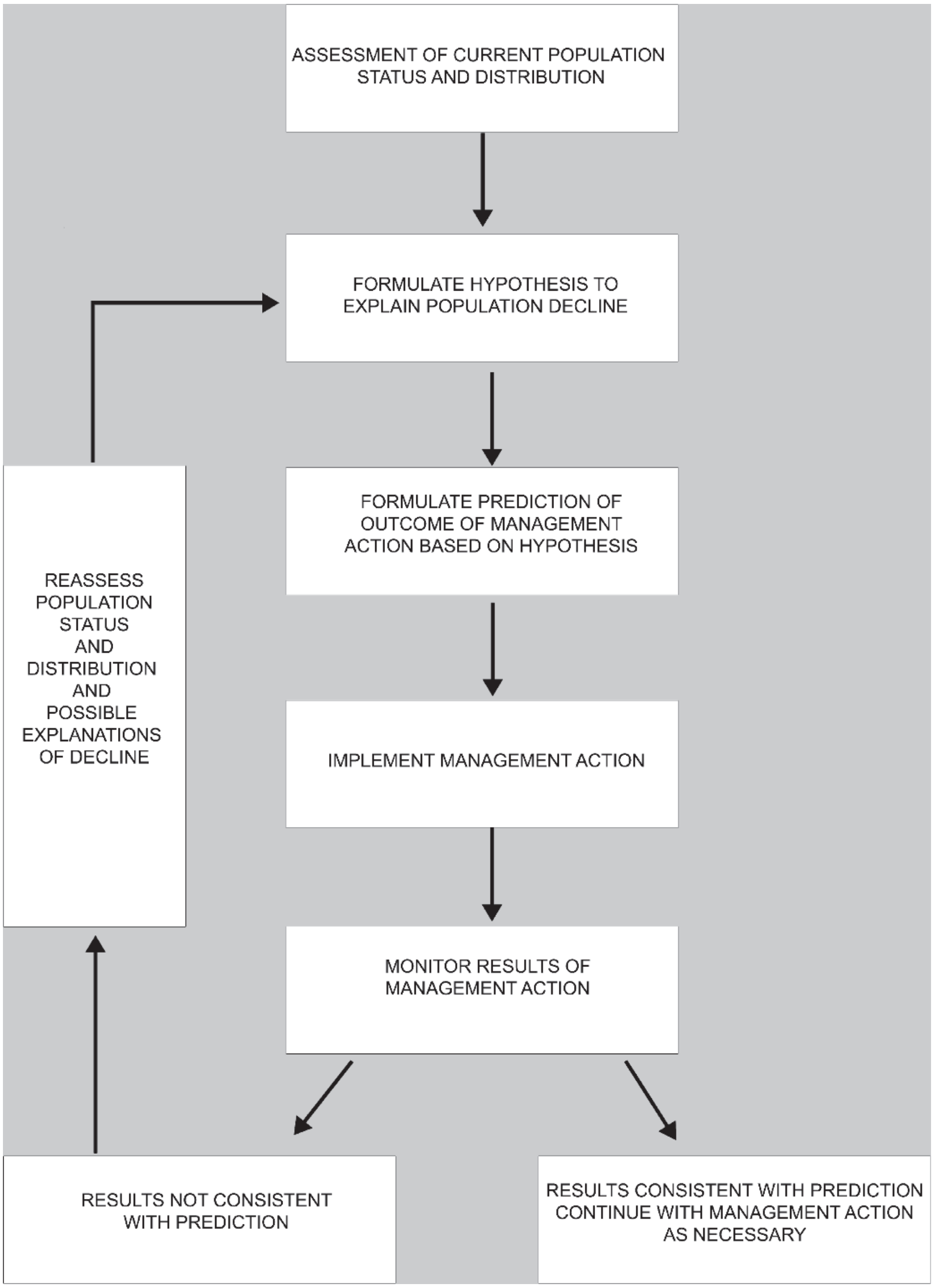

FIGURE 9.4. Schematic flow chart of the analytical and decision-making pathway for developing a management plan for the Lord Howe Island woodhen, a pattern of conceptual analysis and adaptive management that could be applied in other similar situations for small and declining populations needing immediate management intervention.

woodhen and its predators helped construct a hypothesis to explain its decline (pigs limit woodhens), which could be used to formulate a specific prediction (woodhens should increase in number if pigs are removed). That prediction could be evaluated with a management action (eradicate pigs) and the outcomes of the management action compared to the prediction. This sequence of clear thinking and appropriate action saved limited resources (there was no attempt to control other potential predators or competing species) and produced rapid results that could be compared directly to the prediction derived from the hypothesis.

Second, small populations can, in some cases, be helped dramatically by careful, well-planned supplementation of individuals from captive-breeding programs. The release of captive-bred birds in both the mountain area and the areas surrounding the King colony made significant additions to the growth of both populations. As a general principle, individuals raised in wild populations are always preferable for restoration to captive-reared individuals (Chapter 6), but captive breeding programs must sometimes supplement natural reproduction in populations that have reached critically low levels.

Third, the unexpected and fortuitous development of the King colony demonstrates a fact that might have otherwise been overlooked. Small, remnant populations of what was once a widespread species do not necessarily occupy their optimal habitat as they approach extinction. Indeed, forces causing their decline (in this case, pigs) may be driving the last individuals into marginal habitats where survivorship and fecundity are low. In this case, it appears the high-elevation forests were not optimal habitat for the woodhen, but refuge habitat. It is a common and repeated observation of studies of animal behavior that habitat preferences change in the presence of predators, and that habitat that is optimal for breeding is usually not optimal for refuge and escape (Rosenzweig 1991). Thus, conservation biologists should not necessarily assume the habitat occupied by the last remaining individuals in the population is the best habitat for reintroduction. In addition to consulting older, historical data on the population's distribution, a better method might be to use an adaptive management approach. Specifically, attempt reintroductions in multiple habitat types in a more experimental manner and monitor the results carefully over time. There are, in fact, experimental approaches and methods for *in situ* populations that can help managers more systematically investigate the causes of population decline and its potential remedies. We now examine two such approaches, trend analysis and factor resolution.

POINTS OF ENGAGEMENT – QUESTION 1

With the benefit of hindsight, design an experiment that would have determined one important dimension of habitat preference in the Lord Howe Island woodhen. State your research hypothesis, experimental design, and test consequence.

9.1.5. Trend Analysis and Factor Resolution: Systematic Approaches for Identifying Causes of Population Decline and Strategies for Restoration

So far, we have seen, in this chapter and Chapter 8, how population decline and potential restoration can be investigated through long-term studies and associated models of population viability analysis and through quick-thinking and insightful adaptive management strategies that can save a species on the brink of extinction. Is there a viable middle ground between these two extremes? Can we determine, with relatively short-term field experiments, the factors leading to a population's decline and the management treatments that could be most effective in its restoration? To answer this question, we must begin to think about how to adapt experimental design schemes to specifically target demographic factors and address, with clarity, the effectiveness of potential restoration strategies. Let us think through the problem we are trying to solve.

Restoring individual populations of plants or animals normally addresses one of two conditions. One is the restoration of threatened or endangered populations. The other is the restoration of more common species on sites from which they have been exterminated or to sites where they were not historically present but are expected to do well. In the first case, the goal is usually to preserve existing populations *in situ* and, through various management and protective measures, create an environment in which the population increases to levels at which it will no longer be in imminent danger of extinction. These types of restoration efforts typically follow a five-part process:

1. Inventory: a geographically based assessment of rare taxa that documents their existence within mapped political units
2. Survey: an ecologically based assessment of populations in the field that identifies their habitat(s) and endangerment factors
3. Habitat protection: an application of land use restrictions that can be applied, negotiated, or that generate the least political resistance to benefit the endangered population(s)
4. Management; deliberate human actions taken to remedy a deficiency or limitation that is causing the population to decline or remain small
5. Monitoring; systematic measurement of population processes over time
6. Recovery; a point at which the population reaches a numerical level, with appropriate demographic patterns, such that extinction by natural catastrophe or environmental, demographic, or genetic stochasticity is no longer likely

The simplest form of monitoring involves making regular census or survey data to determine the status of the endangered population. Although this gives an index of the population's status, it cannot and does not tell us the prospects for the population's long-term persistence or the causes of its decline or continuing low levels. Both are essential for successful restoration and recovery. In particular, demographic monitoring is the most effective method for determining both the probability of persistence and the causes of decline or chronically low population levels. Demographic monitoring is not census or survey data. Rather, demographic monitoring uses some method of following the fates of individuals in the population over time, as described in previous examples like the studies of the western prairie fringed orchid and Arizona cliffrose, and makes repeated on site measurements to do so. Two monitoring tools are most important to provide a means to develop experimental approaches and appropriately evaluate data generated in ways that provide insight into potential causes and solutions of population decline and endangerment. One is trend analysis and the other is factor resolution (Pavlik 1994).

Trend analysis calculates one or more specific demographic variables in one or more populations and, from such calculations, determines if the population is growing, stable, or declining. As in population viability analysis generally, one of the most common measures in trend analysis is λ, the populations' finite rate of increase. We have already seen (Chapter 8) the use of lambda to assess trends in endangered species populations. Population Viability Analysis is, in fact, an integrated form of trend analysis in which multiple demographic variables are used to estimate the probability of a population of a specific size persisting for a specified time period.

Trend analysis alone cannot identify the exact cause of the population's low numbers or decline, but it can lead to intelligent guesses about what kinds of factors to investigate. Some general, non-mathematical indicators of population stability can be used with trend analysis to make an intelligent assessment as to whether an introduced plant population is stable and likely to persist at its new site (Table 9.1). A plant population with high rates of annual adult survivorship but chronically low rates of seed germination would suggest that environmental variables affecting seeds, such as soil moisture, seed predation, or soil temperature, may be more important to the population than factors affecting adult plants, such as ambient temperatures, herbivory, or competition. For example, trend analysis of populations of the large-flowered fiddleneck (*Amsinckia grandiflora*), an endangered annual forb (Family Boraginaceae) native to dry grasslands of California (USA), indicated that competition with other plant species was the primary limiting factor in population recovery (Pavlik 1994). Thus, a suggested management strategy was to treat sites where *Amsinckia grandiflora* occurred in ways that would remove more common, competing species. The two most commonly used treatments to remove competitors were herbicides (which killed surrounding grasses) or prescribed burning. Figure 9.5 shows the experimental design, derived from such trend analysis, that Bruce Pavlik and his colleagues used to determine which treatment had the greatest effect on populations and Table 9.2 the results of the experiment (Pavlik et al. 1993). We see from this example how trend analysis can guide the second phase of demographic monitoring, ***factor resolution***. In factor resolution, experimental tests of one or more factors suspected of limiting population growth are conducted in the field. The results help to determine which factors limit population growth, and allow managers to determine which variables to manipulate for the best chance of population recovery.

As noted above, the second type of problem in population restoration is to create new populations on a site where they do not exist. Here, the manager begins with factor resolution and ends with trend analysis. Experimental tests are conducted to identify factors limiting the growth of the population. The results are then used to determine the trajectory of population growth and what, if anything, ought to be done to enhance it. Again, studies of the large-flowered fiddleneck provide a clear example. In this species, the long-term goal was to restore this species to California grasslands where it was no longer present. But for such restoration to work, some competition between the fiddleneck and other plants would be inevitable. Ideally, most conservationists would

TABLE 9.1. Demographic parameters that serve as general indicators of population stability in analysis of trends in endangered plant populations.

Parameter	Life Form	Population Stable if
Survivorship	Annual	Mortality inflection point on survivorship curve (Type I) follows onset of seed production.
	Perennial	The number of individuals in a new cohort equals or exceeds the number of extablished individuals after inflection point on survivorship curve (Type III).
Seed bank	All	Density of viable seeds in soil prior to season of germination far exceeds the average density of established individuals.
	Annuals and herbaceous perennials	Year-to-year changes in density of viable seed are not correlated with changes in the density of established, reproductive individuals.
Seed production	All	Seed production per individual of an endangered taxon equals or exceeds that of a nonendangered relative with similar life form.
Age structure	Perennial	Number of established, reproductive individuals is less than the number of established juveniles and/or the number of recruited seedlings.
Frequency of establishment	Annual	Frequency of establishment is less than the half-life of seeds in the seed bank.
	Perennial	Frequency of establishment is less than the half-life of extablished, reproductive plants.

Source: Based on Harper (1977) as summarized by Pavlik (1994).

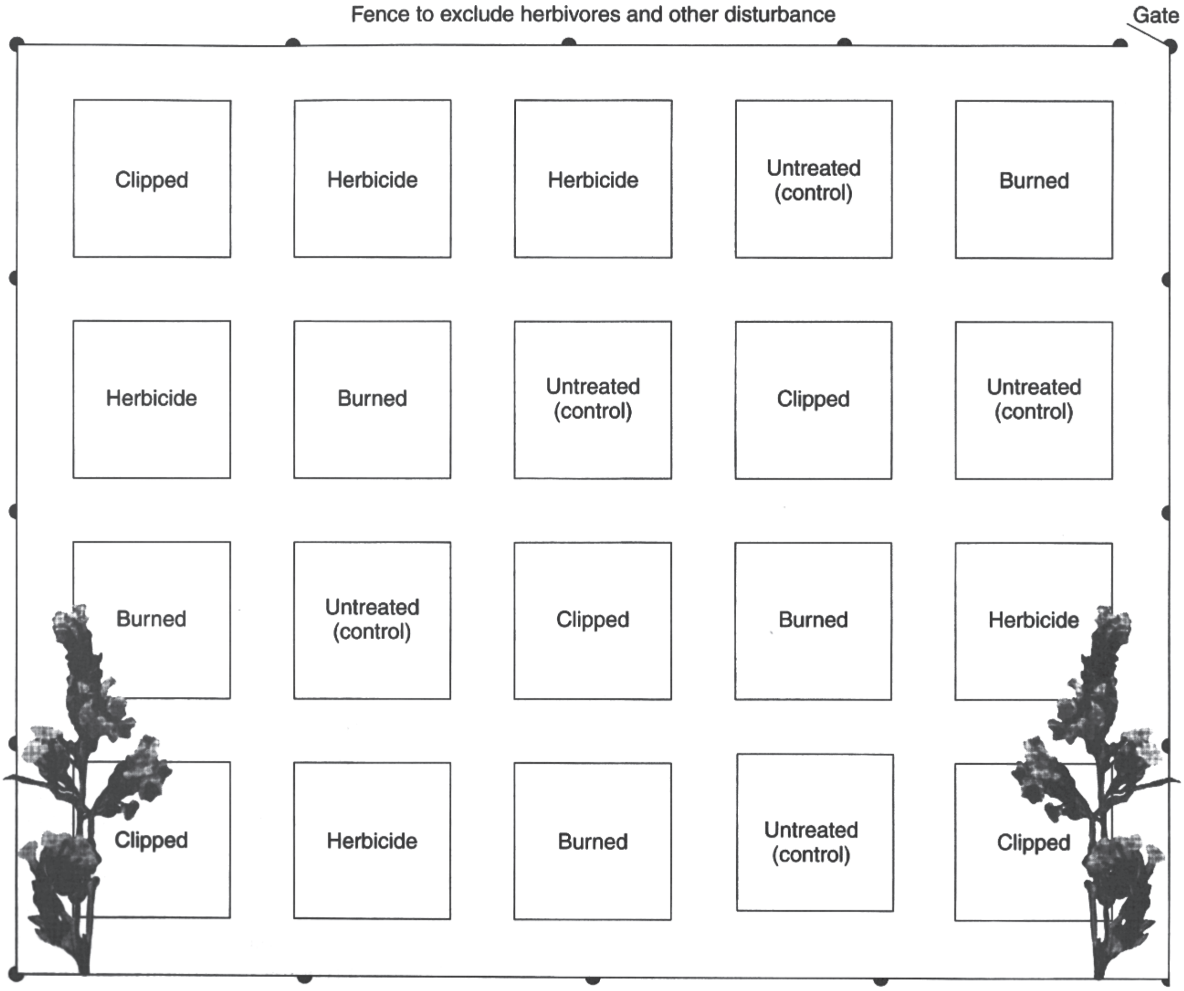

FIGURE 9.5. Experimental design used to create a new population of the endangered plant, *Amsinckia grandiflora*, within its historic range. Each of the 20 plots was either a treatment (burned, hand clipped, or herbicide (Fusilade) treated) or a control in order to measure the effects of competition from non-native grasses. (Based on Pavlik 1994; Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

TABLE 9.2. Results of experimental treatments on germination, population size, survivorship, plant size and nutlet (seed) production of the endangered plant *Amsinckia grandiflora*. Values (mean ± SD) in a column followed by the same letter are not statistically different ($P < 0.05$, ANOVA).

Treatment	Germination	Population Size (Reproductive Plants/Plot)	Survivorship (% of Germination) to Reproduction	Mean Maximum Plant Size (cm)	Nutlet (Fruit) Production (No./Plant)
Control	55.4 ± 5.2a	38.6 ± 15.8a	42.7 ± 16.5a	26.0 ± 3.1a	15.1 ± 10.1a
Burn	55.4 ± 9.9a	67.2 ± 19.8a	75.3 ± 11.6b	33.7 ± 5.3b	29.1 ± 14.4a
Clip	54.1 ± 4.8a	57.8 ± 16.5a	63.1 ± 12.0a	23.1 ± 3.7a	6.6 ± 5.6a
Herbicide	54.0 ± 8.1a	56.4 ± 15.6a	64.4 ± 10.8a	40.5 ± 4.1b	53.5 ± 16.5b

Source: Data from Pavlik et al. (1993).

want to achieve restoration of the fiddleneck within historic native grassland communities of indigenous species. Could the fiddleneck also persist when planted with non-native exotic grasses, and would its competitive abilities differ in different settings?

To take their research to the next step in answering this question Pavlik continued the study with Tina Carlsen and John Menke by determining the performance of *Amsinckia grandiflora* in native grasslands dominated by a perennial species, Sandberg bluegrass (*Poa secunda*), compared to exotic, mostly annual, non-native grasses at low, medium, and high densities of grass. Using the number of inflorescences (flower heads) on individual fiddlenecks as an index to reproductive performance, Carlsen et al. (2000) found that both types of grasslands reduced numbers of fiddleneck inflorescences at high grass densities, but native grasses reduced fiddleneck inflorescences less at low and intermediate densities (Figure 9.6). Carlsen et al. hypothesized that the difference may be due to differences in growth forms in the grasses. Whereas the non-native grass species tended to form a relatively solid mat with few openings, Sandberg's bluegrass and other native grasses grew in well defined clumps (tussocks) with openings between clumps, especially at low and intermediate densities (Carlsen et al. 2000). Based on these findings, the investigators concluded that "restored native perennial grasslands of intermediate densities have a high habitat value for the potential establishment of the native annual *A. grandiflora*" (Carlsen et al. 2000:18). Together, these studies of the large-flowered fiddleneck illustrate how well-designed experiments incorporating factor resolution and trend analysis can inform management decisions that are more likely to lead to successful conservation efforts.

Although some restored populations remain chronically small and require the use of trend analysis and factor resolution to determine the means to increase population sizes, there are notable exceptions to this pattern. In some cases, chronically small populations have increased in number and distribution, not through direct introduction of populations but through an array of indirect factors such as legal protection, changing public attitudes, and altered regional habitat distribution. In these cases, restored populations may increase to the point that control of the population must be considered.

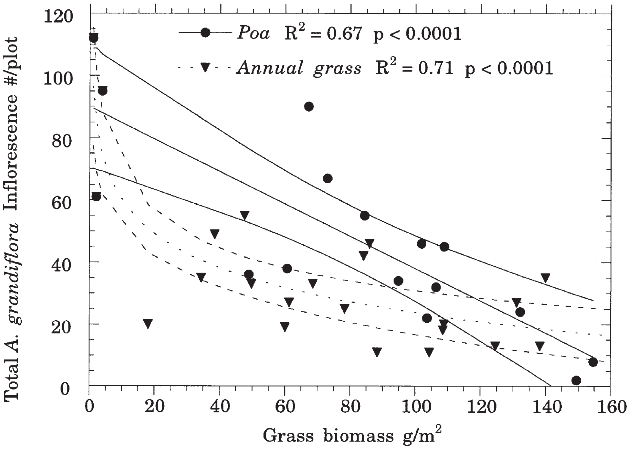

FIGURE 9.6. Relationship of *Amsinckia grandiflora* total inflorescence number per plot (measured 12 April 1994) to final dry grass biomass (measured 1 May 1994), showing predicted means (middle lines) and 95% confidence intervals (outer lines). (Carlsen et al., Reducing competitive suppression of a rare annual forb by restoring native California perennial grasslands, *Restoration Ecology*, Copyright 2000 by Blackwell Publishing.)

POINTS OF ENGAGEMENT – QUESTION 2

Consider the data in Table 9.2. All three management treatments are designed to achieve the same result – increased populations of *Amsinckia grandiflora* through elimination of competing species – but achieve it through different means. Which treatment or combination of treatments would you use to achieve the largest population?

9.1.6. The Gray Wolf: A Case History of Natural Population Restoration

The gray wolf, once widely distributed throughout North America, was exterminated throughout most of the United States, except Alaska, by the early 1900s. A remnant population persisted in northeast Minnesota. With the passage of the US Endangered Species Act (ESA) of 1973, the wolf received protection as a threatened species in Minnesota and as an endangered species in the rest of the conterminous US. Protected by the ESA, the Minnesota population nearly tripled between 1973 and 1997, increasing from 700 to 2,000 individuals (Fuller et al. 1992; Mladenoff et al. 1997).

By the late 1970s, biologists began to observe that wolves were expanding their range to the neighboring regions of northern Wisconsin and Upper Michigan (Mladenoff et al. 1997) and the Michigan and Wisconsin populations had each reached 100–150 individuals by 1997 (Haight et al. 1998). With increasing numbers, researchers also observed that wolves were moving into more-developed areas with higher road densities and human populations, and a landscape with an increasing proportion of private property (Fuller et al. 1992; Haight et al. 1998). Such expansion coincided with two developments, in addition to legal protection, that aided population growth. First, the public became more favorable to the presence of wolves, leading to less frequent illegal shootings. Second, changes in regional forest management, especially the creation of young, intensively managed forests with many openings, led to increases in populations of the wolf's primary prey, the white-tailed deer. This triumvirate of legal protection, public support, and abundant prey created favorable conditions for wolf population growth, with exponential increases in populations in all three states (Figure 9.7).

Expanding wolf populations in the upper Great Lakes region have forced rethinking of traditional wisdom about wolves. Once considered a symbol of wilderness, wolves in this region are now moving southward into areas with higher human densities and more altered habitats. Wolf researchers Mladenoff et al. wrote, "Recent research and monitoring of wolf behavior … and recent wolf population growth have shown that wolves are not the wilderness species they were once assumed to be. … If wolves are not

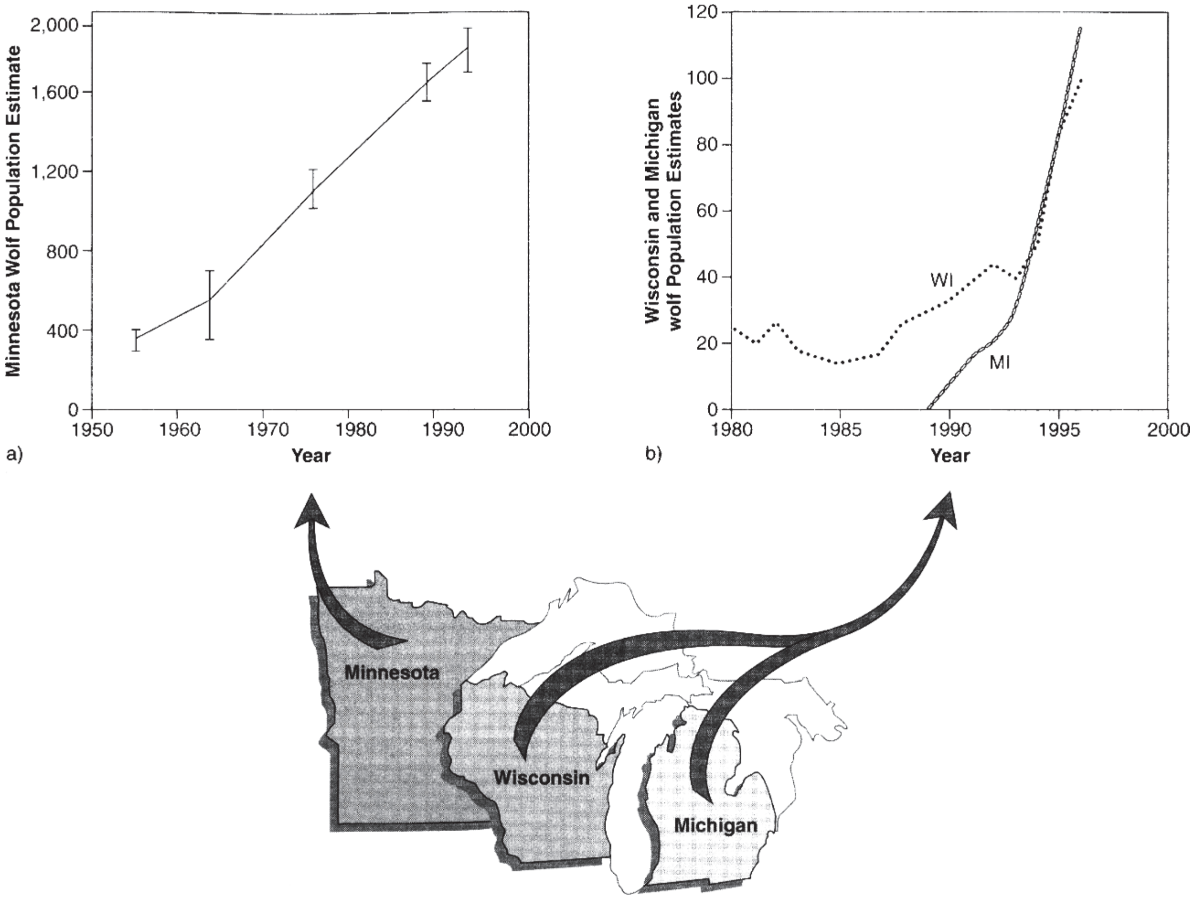

FIGURE 9.7. Estimated recent wolf population growth in Minnesota (a), and Wisconsin and Michigan (b) (USA). (After Mladenoff et al. 1997; Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

killed, and ungulate prey are adequate, they can apparently occupy semi-wild lands formerly thought to be unsuitable. Our work and that of others suggests that current population growth will continue and that dispersal ability and adaptability of wolves will allow them to colonize increasingly developed areas" (Mladenoff et al. 1997). Complementing the field studies, a simulation model of these populations indicated that wolves in the upper Great Lakes states could survive and grow as disjunct populations (metapopulation subunits, Chapter 8) in semi-wild areas as long as prey was abundant, human persecution was not excessive, and wolves could move freely between different populations (Haight et al. 1998). As Robert Haight and his colleagues who developed the model noted, "Our simulations imply a favorable outlook for the survival of disjunct wolf populations" (Haight et al. 1998:885).

The gray wolf in the US upper Great Lakes region was officially delisted (Chapter 3) as an endangered species by the US Fish and Wildlife Service on 29 January 2007. Its recovery is no longer the prediction of a simulation model, but a real event. But that recovery is an incubator of two developing and related conundrums in population restoration. First, if wolf populations continue to grow, negative interactions with humans, particularly involving livestock and pets, are certain to increase (Mladenoff et al. 1997). This prediction has proved true. Since the late 1990s, wolf numbers have continued to rise in the upper Great Lakes states of the US, and wolf predation on livestock has increased in northern Minnesota and northern Wisconsin. Based on a spatial model developed from known predation sites, the livestock most at risk are those in areas with high proportions of pasture and high densities of white-tailed deer, which suggests that wolves may be opportunistic predators or livestock rather than dependent on them. Other risk factors, acting through inverse relationships, were areas with low proportions of crop lands, coniferous forests, herbaceous wetlands, and open water. Large farms with greater numbers of livestock in areas of low road density also appeared to be more vulnerable (Treves et al. 2004).

Where livestock predation and other forms of wolf–human conflicts continue to increase, the most obvious and direct management strategy is to kill wolves. Adrian Treves and his colleagues, after completing the development of their wolf–human interaction model, suggest that "… public hunting of wolves might be directed to areas with high expected rates of conflict to limit the severity of conflict and maintain the state wolf population at politically acceptable and established levels" (Treves et al. 2004:124). But, at the moment, only authorized government agents are legally permitted to control (kill) wolves. As L. David Mech, one of North America's leading authorities on the wolf, points out, the wolf could live in far more places than it does today if this control (killing) could be carried out by the public (private landowners protecting their own livestock) instead of exclusively by government officials (Mech 1995). Indeed, a larger segment of the public would find the wolf an acceptable species where they actually live if they had some role in wolf control. Ironically, most wolf conservationists would never support this arrangement, preferring that wolf populations not grow rather than move into, or be restored to, areas where control, particularly public control, would be necessary. As Mech skillfully puts it, "some people revere wolves so much that, rather than having wolves face control, these people would rather not restore wolves to areas where they would have to be controlled," (Mech 1995). It was growing concern over this kind of conflict that motivated Adrian Treves and Lisa Naughton, to establish a unique conservation NGO, COEX, whose mission is to promote the coexistence of people and wild animals. "We study and solve conflicts," note Treves and McNaughton, "that threaten human security and wildlife populations at home and around the world. Our approach to conflicts integrates strategic planning of conservation with thorough consideration of the human dimensions of environmental problems" (COEX 2007, http://www.coex-wildlife.org/about.htm).

In addition to the issues associated with direct wolf–human conflicts, there is another problem of equal concern to conservation biologists associated with wolf restoration. The increasing deer densities needed to support wolf populations would reduce the biodiversity of the understory forest community and reduce recruitment of some tree species (Mladenoff and Stearns 1993; Alverson et al. 1995). The Forest Service has been sued by botanists on this issue (Mlot 1992) and is increasingly inclined, in cooperation with state agencies, to institute management programs that will reduce deer populations. If deer densities decline, so will wolf productivity and pup survival (Fuller et al. 1992). As a result, wolf numbers and ranges could be expected to contract.

The ongoing success of wolf restoration illustrates two principles inherent in population restoration efforts that often receive inadequate consideration. First, the creation of a legal, social, and ecological climate favorable to a species may have more impact on its recovery than direct manipulation of the population. Second, managers would be prudent to determine, in advance, an acceptable maximum population and range for restored and recovering populations before they reach levels that produce negative interactions with humans, habitat degradation, loss of biodiversity, or steep declines in populations that could pose new threats to population persistence. It is precisely the success of this restoration that creates one of the most intriguing paradoxes of conservation, one generated by humanity's own incongruity of belief and behavior. If we truly desire restored ecosystems and their species to be part of everyday life, we must be prepared to alter our attitudes and actions for such restoration to be successful. Traditionally, conservationists have affirmed this sentiment, always assuming that it meant that non-conservationists would have to alter their "bad" opinions and behavior to allow for the presence of other species. But population restoration is a dangerously reciprocal process, and conservationists, as well as non-conservationists, must accept some limits on non-human species if they would see those species become a more permanent part of a landscape in which humans reside.

9.2. Invasive Species: Threats to Native Biodiversity

9.2.1. General Considerations

In a world of increasingly mobile human populations, it is not surprising that such human movement has been accompanied by increasing numbers of invasions of other, non-native species, to many parts of the world where they were not previously found. Today the effects of non-native species are the second most commonly listed factor contributing to endangerment after habitat loss and degradation. Regrettably, the human role in spreading such species has often been deliberate in its intent while ignorant of its consequences. In the nineteenth century the Naturalization Society in New Zealand attempted, and for the most part succeeded, in re-creating the ambience of an English countryside in some parts of New Zealand by releasing common British songbirds, often to the detriment of the native birds (Godfray and Crawley 1998). But even more introductions are accomplished simply by human ignorance, as people, along with their goods, clothes, and transport vessels, serve as the conduits for plant and animal stowaways carried unnoticed throughout the world. Generally, invasive species reach new environments either through human commerce in living organisms (what might be called "intentional introductions") or through unintended transportation as "stowaways" in ships, planes, trains, and automobiles or in the packages or ballast they are carrying, or, especially in aquatic invasions, through human-created conduits like canals or pipelines that connect formerly disconnected areas (Figure 9.8). In aquatic invasions, whole non-native communities of creatures attached to the bottom of ships or living in the ballast

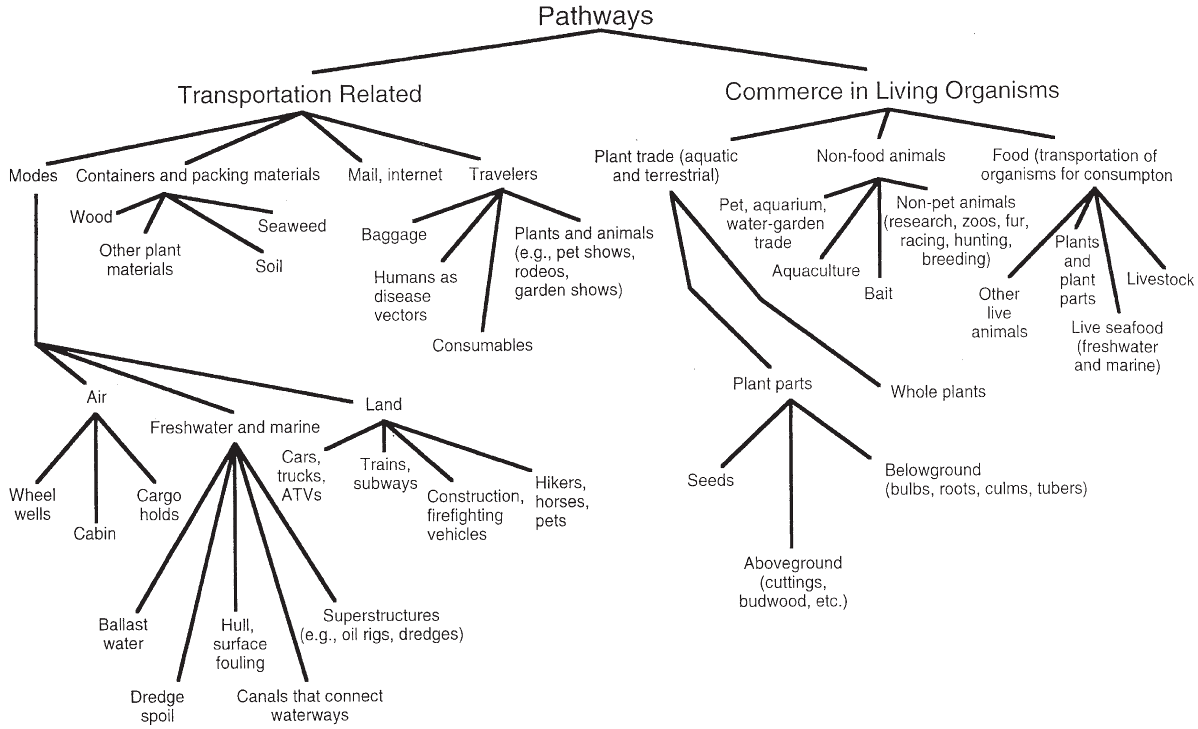

FIGURE 9.8. The major pathways through which non-native species enter new areas, countries, or regions and are transported within them. The right-hand pathway of commerce in living organisms also assumes the left-hand pathway of "stowaway introductions" because commerce in selected species entails the possibility of other species "hitchhiking" with the selected species, as well as the possibility of misidentification of selected species at the point of origin or delivery, or both. (Lodge et al. 2006. Biological invasions: recommendations for U.S. policy and management and management. *Ecological Applications* 16:2035–2054. Reprinted by permission of the Ecological Society of America.)

water of such vessels may be transferred at once to new environments (Ruiz et al. 1997). Many species of insects may move throughout the world in processed or unprocessed wood products, while others that feed on vegetables and fruits, such as the Mediterranean fruit fly or "medfly" (*Ceratitis capitata*) often move worldwide as adults or larvae in produce shipments (Carey 1996). Plants may be dispersed long distances as spores or seeds, or actively collected and planted under cultivation, only to later escape to the wild. And humans, including conservation managers, still introduce plants into public and private lands, preserves and wildlands in some areas in efforts to revegetate sites affected by fire, erosion, or overgrazing, or to enhance forage production for wild or domestic herbivores.

It is difficult to assess the total number of non-native species worldwide or their rates of invasion, as estimates vary according to phylogenetic group and reference time frame. From their own research and reviews of other sources, forest scientist Pekka Niemelä and insect ecologist Willliam J. Mattson have concluded that nearly 2,000 species of insects and 2,000 species of weedy plants have invaded North America in the last 500 years (Niemelä and Mattson 1996). Godfray and Crawley (1998) have estimated that at least 20,000 non-native plant species have been introduced into Great Britain, nearly 1,200 of which have become naturalized. Among aquatic organisms, Carlton and Geller (1993) list 46 species of non-native species that have been introduced around the world from ballast-water discharges just since the 1970s. In the United States, 50,000 non-native species are estimated to have been introduced, and their estimated environmental and economic cost was estimated in 2005 at US$120 billion per year (Pimentel et al. 2005) (Table 9.3).

Most introduced species fail to establish persistent populations, and most of the successful ones that do live inconspicuous lives among the natives. Some, including many kinds of crop plants, are beneficial. But a small number experience enormous population growth and range expansion, often with devastating ecological and economic effects on the native communities. Although details and specifics vary on a case by case basis, we can generalize a predictable pattern of successful invasion characterized by seven distinct stages (Figure 9.9): introduction (intentional or accidental), colonization (sustained residence on at least one new site), establishment (positive population growth on one or more new sites), dispersal, spatially distributed populations, invasive spread, and adaptation to the new environment. Whether benign or pestilent, such invasions cause changes in community composition, structure and function. Indeed, it is impos-

Table 9.3. Estimated annual costs associated with some alien species introduction in the United States. Numbers × millions of US dollars.

Category	Nonindigenous species	Losses and damages	Control costs	Total
Total				
PLANTS	25,000			
Purple loosestrife		–	–	45
Aquatic weeds		10	100	110
Mealeuca tree		NA	3–6	3–6
Crop weeds		24,000	3,000	27,000
Weeds in pastures		1,000	5,000	6,000
Weeds in lawns, gardens, golf courses		NA	1,500	1,500
MAMMALS	20			
Wild horses and burros		5	NA	5
Feral Pigs		800	0.5	800.5
Mongooses		50	NA	50
Rats		19,000	NA	19,000
Cats		17,000	NA	17,000
Dogs		620	NA	620
BIRDS	97			
Pigeons		1,100	NA	1,100
Starlings		800	NA	800
REPTILES and AMPHIBIANS	53			
Brown tree snake		1	11	12
FISH	138	5,400	NA	5,400
ARTHROPODS	4,500			
Imported fire ant		600	400	1,000
Formosan termite		1,000	NA	1,000
Green crab		44	NA	44
Gypsy moth		NA	11	11
Crop pests		13,900	500	14,400
Pests in lawns, gardens, golf courses		NA	1,500	1,500
Forest pests		2,100	NA	2,100
MOLLUSKS	88			
Zebra mussel		–	–	1,000
Asian clam		1,000	NA	1,000
Shipworm		205	NA	205
MICROBES	20,000			
Crop plant pathogens		21,000	500	21,500
Plant pathogens in lawns, gardens, golf courses		NA	2,000	2,000
Forest plant pathogens		2,100	NA	2,100
Dutch elm disease		NA	100	100
LIVESTOCK DISEASES		14,000	NA	14,000
HUMAN DISEASES		NA	7,500	7,500
TOTAL				$120,105

Source: Pimentel et al. (2005). Copyright Elsevier 2005. Used with permission of Elsevier.

sible to understand existing communities worldwide without an understanding of species' introduction and invasion. Thus Godfray and Crawley assert that "… the composition of many (perhaps even most) communities is determined by the history of introduction" (Godfray and Crawley 1998).

An understanding of invasive species takes on especial urgency in conservation because such exotic introductions, invasions and establishments often displace or even eradicate native species, especially species with small populations, specialized habitat requirements or limited range. For example, cheatgrass a European grass introduced to the US, has invaded and spread with particular success through the shrub-steppe ecosystem of the western US Great Basin region in the states of Idaho and Utah. In native plant communities dominated by sagebrush (*Artemisia tridentata*), fires burned at a periodicity of 60–110 years. In areas dominated by cheatgrass, fires burn every 3–5 years, reducing reestablishment of sagebrush and other shrubs (Pimentel et al. 2005), and destroying habitat for sagebrush obligate species like sage grouse and Brewer's sparrow.

Introduced species reduce biodiversity not only through competition but also predation. Predation is often most devastating to a prey species when an introduced predator encounters native prey species that have evolved few or no defenses against it. A classic example of extinctions caused solely by the actions of an introduced predator

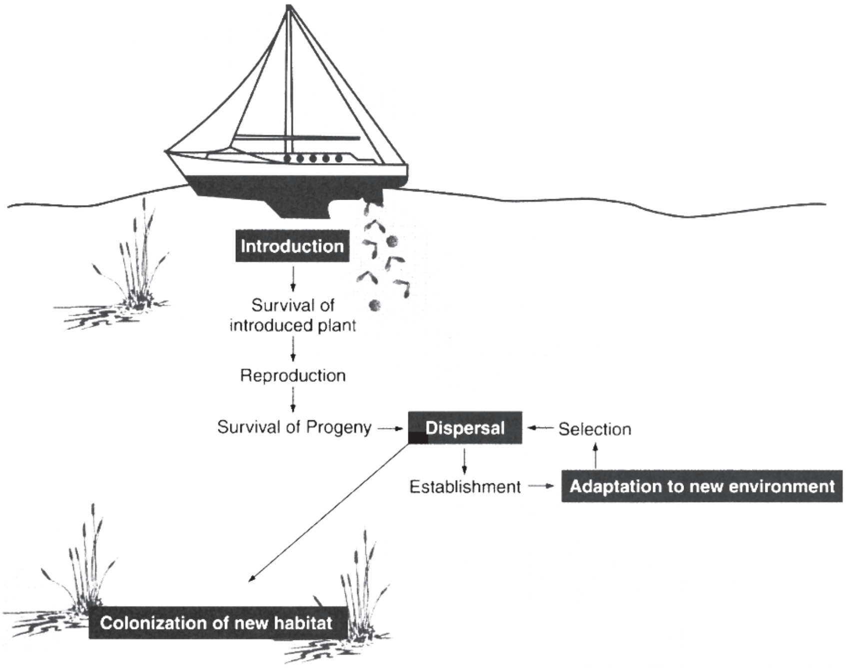

FIGURE 9.9. The process and stages associated with the invasion, establishment, and spread of a non-native species. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts*, *Applications,* Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

FIGURE 9.10. The brown tree snake (*Boiga irregularis*), an introduced predator to the Pacific island of Guam, that has exterminated all species of native birds. (Photo courtesy of John Fowler.)

is the case of the brown tree snake (*Boiga irregularis*) (Figure 9.10), which reached the Pacific island of Guam in 1967. The snake's spread coincided with the disappearance and extinction of three species of birds native to the island; research confirmed that the snake – the only predator unique to Guam – was indeed the cause. Some species are neither competitive nor predatory, but create such pervasive changes in vegetation and habitat that indigenous species cannot survive. For example, pigs and goats from Europe have devastated native flora and fauna of tropical islands throughout the world where they have been introduced.

Such stories of non-native species invasions and their effects make for fascinating reading, and comprise the entire content of many excellent books (e.g. Elton 1958; Pimentel 2002; Mooney et al. 2005; Sax et al. 2005). However, our purpose here is not to tell every story of alien invasion, but to explicate patterns, principles and theories regarding such invasions in general that we may better understand individual case histories in particular, and thus better respond to and manage non-native populations such that native species are conserved. We begin with a general review of common trends that emerge from repeated patterns of invasion.

9.2.2. Characteristics of Successful Invading Species

No single comprehensive theory adequately explains all patterns of invasion or all characteristics of invasive species. In general, however, successful invaders often show three consistent characteristics. (1) The invading species can deliver seeds, breeding individuals, or other types of propagules at a high rate at an opportune moment for invasion and at a high density to an opportune site or sites. (2) The invading species is able to persist for extended periods at low densities under unfavorable conditions until favorable conditions permit it to grow to higher densities. (3) The invading species is a good "ecologic match" for the environment, and is able to exploit local conditions and abiotic factors that favor completion of its life cycle as well or better than native species.

Many invaders are especially adept in category one. For example, Rejmánek and Richardson (1996) examined the invasive characteristics of 24 species of pine (*Pinus* spp.), 12 of which they classed as non-invasive (planted on at least three continents but never reported as spreading) and 12 as invasive (spreading on at least two continents). After evaluating ten life history traits in both groups via discriminant analysis, they found only three that were significant in classification. These were the square root of mean seed mass, the square root of the minimum juvenile period, and the mean interval between large seed crops. Invasive species had low mass of individual seeds, short juvenile periods, and short intervals between large seed crops. The second and third traits allowed invaders to achieve early and consistent reproduction once established, while the first contributed to higher numbers of widely dispersed seeds. Interestingly, invasive species were all concentrated in the same subgenus (*Diploxylon*), while non-invasive species were all members of a different subgenus (*Strobus*). This dichotomy suggests that, at least in pines, membership in a subgenus might be the first indication of the possible invasiveness of a species (Rejmánek and Richardson 1996).

Other principles also help to explain the success of invaders in multiple contexts. Specifically, in planned introductions, an introduced species is more likely to be successful if (1) more individuals are released rather than less; (2) more release sites are used rather than fewer; and (3) the releases are repeated many times rather than only once (Veltman et al. 1996). Thus, non-native species that can invade in large numbers at multiple sites in repeated efforts will have higher probabilities of success.

Although the second trait, ability to persist at low densities, is undoubtedly important, we know relatively little about the abilities of invasive species in this regard because, at such low densities, they are often undetected. For example, recent evidence suggests that the Mediterranean fruit fly has been able to persist at low population levels in the Los Angeles Basin of California and slowly spread to other locations in the region despite intense efforts to eradicate it (Carey 1996). Along with low densities, some data also suggest that invasive species are adept at enduring long periods of unfavorable conditions. In Great Britain, alien plant species were more likely to show protracted (>20 years) seed dormancy than native species (Godfray and Crawley 1998). Further, successful invaders must be able to increase in numbers when rare, overcoming the Allee effects that normally cause the decline of small populations.

Many invasive species demonstrate the importance of "ecological match" or "pre-adaptation" to a novel environment. Some aspects of ecological match occur at extremely broad levels. For example, among herbaceous plants, the best indicator of ability to invade a new area appears to be latitudinal range (Forcella et al. 1986; Rejmánek 1995). The greater the spread of latitude (and, by inference, climatic conditions) that an herbaceous plant can tolerate in its indigenous range, the more likely it is to invade new areas. Paralleling this pattern in plants, Niemelä and Mattson (1996) determined that one reason European phytophagous insects are more likely to be successful invaders of North American forests than vice versa is because such forests possess broader capacities to accommodate new host species.

Structural habitat components also appear to play a major role in creating an ecological match that facilitates invasion success in some groups of organisms. In an extensive review of non-native fishes in California, Moyle and Light (1996) determined that abiotic conditions in streams, not characteristics of native biotic communities, were the most important determinants of successful invasion (Moyle and Light 1996). The most successful invaders were those adapted to the local hydrologic regimes, specifically to patterns of seasonal changes in water flow. The investigators concluded "… the most important factor determining the success of an invading fish is the match between the invader and the hydrologic regime" (Moyle and Light 1996).

Another dimension of ecological match is seen in species that can in some way alter the habitat itself, effectively creating their own niche where one did not previously exist. An example of this can be seen in the nitrogen-fixing tree *Myrica faya*, an invasive species on the US island of Hawaii. *Myrica faya* is adept at colonizing volcanic ash and open native forests, both of which are nutrient limited systems. In these systems, *Myrica faya* can increase inputs of nitrogen up to four times (Lodge 1993). One would think that such nitrogen additions might be beneficial to native species in these nutrient-limiting environments. However, for many species, the effects of shading and high rates of litter accumulation under and around *Myrica faya* outweigh these benefits and lead to their decline (Lodge 1993). Thus, *Myrica faya* alters the habitat by changing rates of nutrient cycling as well as the physical structure and light penetration of open forests, creating a new niche favorable to itself but one in which native species cannot survive.

9.2.3. Invasive Species Alter Native Habitats

The problem of invasive species is a worldwide concern affecting all types of environments, but aquatic habitats are especially sensitive to foreign invaders. Freshwater environments are particularly vulnerable to invasion if recently disturbed, if predators are absent, or if effective competitors of the invader are absent (Ashton and Mitchell 1989). Such environments also often harbor disproportionate numbers of endemic, threatened and endangered species. In the US, for example, 67% of freshwater mussels are vulnerable to extinction or already extinct, 51% of crayfish species are imperiled or vulnerable, and 37% of fish species are at risk (Chaplin et al. 2000).

Human transference of species, whether deliberate or accidental, is the primary vector for aquatic species invasions. In analysis of the history of 316 species of nonnative aquatic invertebrates and algae established in North America, Fofonoff et al. found that 251 species invasions (79.4%) included shipping as a possible vector, and 164 (51.9%) species invasions could be attributed solely to shipping (Fofonoff et al. 2003). Aquatic plant species also can be particularly successful invaders because they can survive unfavorable conditions for extended periods of time and are readily transported by biological agents such as birds, fish, and insect. Almost all invasions of plants that have caused significant habitat alteration and other problems, however, have been human-mediated. Assessing the history of invasions by aquatic plants, Ashton and Mitchell commented, "… we have seen that few aquatic plants are dispersed between unconnected water bodies by natural mechanisms. Indeed, more initial introductions of aquatic plants to new continents have been deliberate in that the introduced species was perceived to have some special attraction and/or intended use for humans.… In every case, man has been implicated in their deliberate or accidental introduction to continents outside their native range" (Ashton and Mitchell 1989). The list of such invaders and their natural and introduced histories, including Eurasian water milfoil (*Myriophyllum spicatum*), purple loosestrife (*Lythrum salicaria*), water hyacinth (*Eichornia crassipes*) and others are beyond the scope of this chapter. But the invasive plants tended to have certain traits in common. First, vegetative reproduction was their common, if not exclusive method of propagation. Second, human activity and transport was their main means of dispersion. Third, all were species capable of extremely rapid reproductive rates. The majority of successful invaders also had free-floating life forms (Ashton and Mitchell 1989). Aquatic invaders, such as purple loosestrife, may rapidly invade shallow water habitats, especially wetlands, forming dense stands that choke out native species. Water hyacinth, in contrast, is an emergent species that can form dense mats in deeper water, but with the same result. Eurasian water milfoil is a perennial aquatic herb with a slender, elongate floating stem. Often reproducing vegetatively, Eurasian water milfoil can disperse long distances by floating, and may cling to boats or other manmade structures, facilitating its distribution.

We typically think of animals as being dependent upon plants and their physical environment, but some aquatic animals may radically alter the physical environment itself or even the properties of the surrounding ecosystem. For example, the zebra mussel (*Dreissena polymorpha*) is a classic invasive species with high reproductive rates, wide environmental tolerances, and large dispersal distances. A native of the Black and Caspian Seas in Eurasia, the mussel spread throughout Europe in the nineteenth century. It had reached Lake St. Clair (shared by the US state of Michigan and the Canadian province of Ontario) by 1986, probably arriving via discharges of ballast water from European ships using the Great Lakes via the St. Lawrence Seaway. Downstream dispersion was rapid. By 1991, the zebra mussel was present in New York's Hudson River (USA) and in the St. Lawrence River in Quebec (Canada). Upstream dispersal, facilitated by commercial shipping also occurred. In the US, the species reached the Mississippi River by 1992 via the Chicago Sanitary and Ship Canal. From there the zebra mussel spread through the Mississippi to Louisiana and began to move upstream into the Mississippi's major tributaries (Johnson and Carlton 1996). By 2007, the zebra mussel was present in 23 US states and 2 Canadian provinces, but its westward spread had slowed considerably, and has been less rapid than expected (Bossenbroek et al. 2007). Whereas initial invasions in the US and Canada were facilitated through ballast water discharge, subsequent westward expansion in recent years has been mainly through overland transport of zebra mussles on the hulls of recreational boats, so invasion events have become less frequent. Bossenbroek and his colleagues developed a model to predict the spread of the mussel and its ecological impact on western US waters, and, based on model results, predicted that dispersal to aquatic systems west of the 100th meridian was an event of low probability but potentially high ecological impact (Bossenbroek et al. 2007). The reasons for the zebra mussel's disproportionately large effects on community and ecosystem structure deserve some further and more detailed attention.

The zebra mussel's unique traits exemplify the third quality of successful invaders, that of ecologic match. The zebra mussel, and its European counterpart invader, the quagga mussel (*D. bugensis*) are the only species of mussel on these continents that can attach to hard substrates. Unlike any native species of bivalve in North America or Europe, the zebra and quagga mussels possesses a tuft of filaments ("byssal threads") that allow attachment to any stable surface, even other living creatures. Such a trait not only gives the mussel access to niches that native clams cannot exploit, but also a rapid means of dispersal. The zebra and quagga mussel produce large numbers of plankton-feeding larvae (veligers) that are easily, rapidly, and widely dispersed by prevailing currents.

The zebra mussel is a relatively long-lived species that can actively pump the water it filters while feeding, thus making it better suited than short-lived, passive filter feeders, like insect larvae, to exploit calmer waters associated with lakes and slow moving rivers. An efficient and voracious filter feeder on phytoplankton, models of zebra mussel feeding activities show that, at high densities, zebra mussels can exceed the entire, combined filtering activities of the zooplankton (Johnson and Carlton 1996). At densities now found in western Lake Erie, zebra mussels may remove up to 25% of the system's primary production in phytoplankton *daily*! Taken together, these traits make the zebra mussel a uniquely efficient harvester of planktonic primary productivity. Although such feeding may increase water clarity, it also removes nutrients, energy, and biomass from the pelagic (open-water) portion of the lake community and shunts it to the benthic zone in the form of increased mussel biomass and feces (Brönmark and Hansson 1998). This shift of matter and energy can radically change community composition and species diversity. The effects of the zebra mussel on native species are of particular concern because, as previously noted, 67% of the 297 species of freshwater mussels native to North America are listed as extinct, endangered, threatened, or of special concern (Johnson and Butler 1999; Chaplin et al. 2000). The effects of zebra and quagga mussels on community composition are complex, with some types of species increasing and others decreasing in the presence of these mussels. Ward and Ricciardi (2007) conducted a meta-analysis of 47 published studies of the effects of these two species on aquatic ecosystems in Europe and North America and found a number of consistent patterns. Increasing densities of *Dreissena* had positive effects on densities of scraper and predator macroinvertebrates, especially leeches (Hirudinea), flatworms (Turbellaria), and mayflies (Ephemeroptera), many of which can exploit the filtration currents generated by large colonies of *Dreissena*. Gastropod densities increased overall as *Dreissena* densities increased, but large-bodied snail species declined, as did most large filter-feeding organisms, including sphaeriid clams and burrowing amphipods (*Diporeia* spp.) (Figure 9.11), which *Dreissena* often excludes from substrates they occupy.

Economic losses due to structural damage and clogging of underwater structures such as pipes, is estimated in the millions of dollars. Although initial infestations may reduce water turbidity because of the enormous amount of water collectively filtered by the population, the zebra mussel's combination of high reproductive rate and short life span can eventually lead to the accumulation of large numbers of dead mussels that foul the water (Hayes 1998). They also infest physical structures such as intake and output pipes of shoreline powerplants, clogging these structures to the point that they can now longer function. In 2002, each such infested powerplant in the US was estimated to cost US$3 million to repair (Leung et al. 2002).

Larger non-native species also can radically alter aquatic habitat. The carp (*Cyprinus carpio*), a bottom-feeding fish originally native to Europe, was introduced in the United States in the 1830s and was the subject of massive, intentional introductions to freshwater rivers and streams by the 1890s. Such introductions were treated as celebrations with high hopes for the carp as an outstanding game fish. Bands played. Politicians made speeches. The future outcome was less pleasant than the day's happy events. Tolerant of turbid, poorly oxygenated, even chemically polluted waters, carp proliferated as prophesied, but not to many anglers' delight. Among their other undesirable habits, carp routinely destroy emergent wetland vegetation through their rooting action in the sediment. In controlled experiments in which carp were confined in enclosures, they destroyed up to one-third of all submergent aquatic vegetation. The variation in the proportion of the amount of vegetation

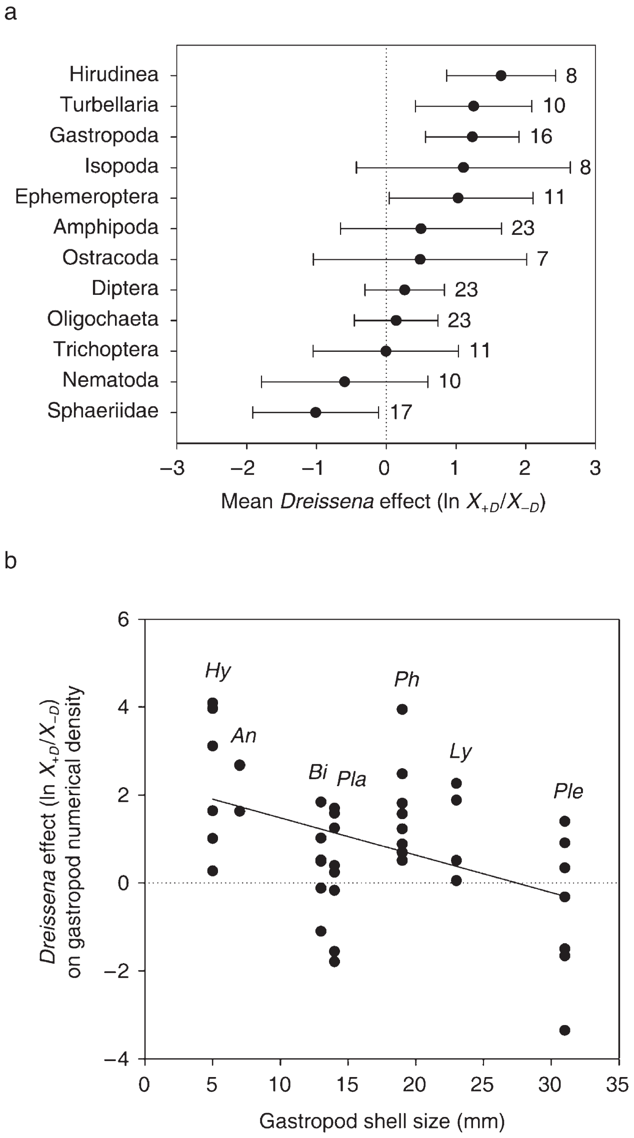

FIGURE 9.11. Effects of changing densities of zebra mussel (*Dreissena polymorpha*) or quagga mussel (*D. bugensis*) on freshwater aquatic invertebrate communities. "*Dreissena* effect" represents the natural log (ln) of the ratio of the effect on the response variable (density of taxa or gastropod shell size) in the presence (X_{+D}) and absence (X_{-D}) of a large colony of *Dreissena*. (a) *Dreissena* effect on the numerical density of major aquatic invertebrate taxons. Most taxons showed increased densities (ln X_{+D}/X_{-D} >0) in the presence of large colonies of *Dreissena*. (b) However, although large *Dreissena* are associated with overall increases in gastropod densities, larger gastropods tend to decline in the presence of *Dreissena*. Data points represent species-specific responses of gastropods arranged in columns by family. *Hy*, Hydrobiidae; *An*, Ancylidae; *Bi*, Bithyniidae; *Pla*, Planorbidae; *Ph*, Physidae; *Ly*, Lymnaeidae; *Ple*, Pleuroceridae. (Ward and Ricciardi, Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: a meta-analysis, *Diversity and Distributions,* Copyright 2007 by Blackwell Publishing. Reproduced with permission of Blackwell Publishing and J. M. Ward and A. Ricciardi.)

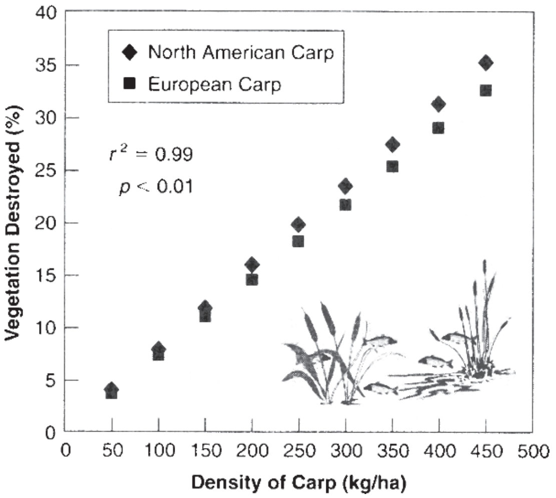

FIGURE 9.12. The effect of carp (*Cyprinus carpio*) on aquatic vegetation in experimental enclosures. The durations of the North American and European experiments were 92 and 71 days, respectively. Vegetation loss increased linearly with increasing carp biomass. (Original data from studies by Robel (1961) in Utah (USA) and Crivelli (1983) in France. Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

destroyed can be almost completely explained by variation in the biomass of carp in the exclosure (Figure 9.12). More remarkably, the pattern of plant destruction was almost exactly the same even when experiments were performed independently on different continents, North America and Europe (Robel 1961; Crivelli 1983).

Some non-native species do not change the habitat itself, but may cause profound changes in the use of habitat by other species. The Nile perch (*Lates niloticus*), a large and voracious predatory fish, was introduced into Lake Victoria in east Africa in 1954 as a food source for human populations to supplement dwindling supplies of native fish. Its populations remained low for nearly two decades, but exploded in the 1980s, to the detriment of many native endemic species in the lake. Lake Victoria's rich biodiversity of haplochromine (*Haplochromis* spp.) cichlids, species found nowhere else in the world, experienced a massive episode of extinction during the Nile perch's population explosion, what some conservation biologists have called "the largest mass extinction of contemporary vertebrates" (Seehausen et al. 1997). Two hundred endemic species of cichlids disappeared (Seehausen et al. 1997). Many of these species, as well as many species that survived, were not randomly distributed in Lake Victoria but concentrated in particular habitats (Figure 9.13). Most extinctions occurred

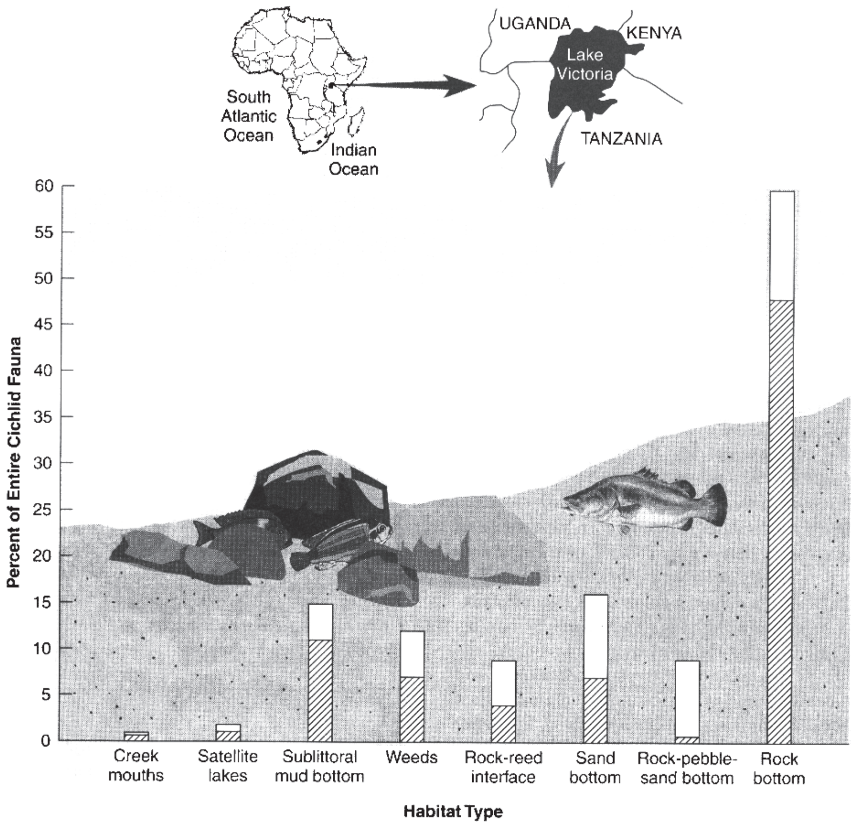

FIGURE 9.13. Proportions of extant haplochromine (cichlid) fauna in eight microhabitats in southern Lake Victoria, Tanzania. Striped portions of bars indicate proportion of species that are restricted to the given habitat. Total bar length indicated proportion of species that use the given habitat as one of their major habitats. The Nile perch (*Lates niloticus*, pictured, right), introduced in 1954, exterminated many species of cichlids, and patterns of extinction were habitat specific. Habitat shifts have subsequently occurred in many cichlid species, apparently as a means of avoiding predation. (Based on data from Seehausen et al. 1997; Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

in sublittoral and weed zones. Many species that survived the introduction of the Nile perch have made major shifts in habitat use. For example, in the pre-Nile perch era, *Haplochromis tanaos* and *H. plagiodon* were restricted to littoral sand bottom habitats on the east side of Lake Victoria's Mwanza Gulf (Witte et al. 1992). In the 1990s, after the Nile perch had reached large population levels, these species were found in littoral and sub-littoral mud bottom habitats on the west side of Mwanza Gulf (Seehausen et al. 1997). Such habitat shifts are consistent with a general pattern of habitat selection well documented in other studies of terrestrial and aquatic species and predicted by theoretical models of habitat selection – namely, that, in the presence of a predator, individuals shift from optimal foraging habitat to optimal cover habitat, or to any habitat where the predator is not present (Rosenzweig 1991). The population survives, but growth and reproduction are reduced. Managers must consider that, if non-native predators enter a system, habitat management and conservation strategies may have to be altered to preserve biodiversity.

9.3. Managing Invasive Species: Prediction, Response, and Restoration

9.3.1. The Problem of Prediction: Can We Construct Models of Invasive Patterns to Understand the Invasive Process?

The identification of common trends and traits in invading species is helpful in understanding the processes through which non-native species become established in new environments. Such identification of common traits and processes may assist a conservation biologist in making a preliminary assessment of which potentially invasive species have the greatest probability of success, and the greatest potential for harm. Better still would be the ability to model the invasion process in a systematic manner, and thus gain even greater understanding of its mechanisms and the ability to make even more specific predictions about its outcomes. Despite our best scientific and management efforts, we still are unable to successfully predict the most important aspects of biological invasions, which include (1) the conditions under which a species will become invasive, (2) the attributes that make some species more invasive than others, and (3) the ecological and population dynamics of the invasions themselves (Mack et al. 2000).

Scientists concerned with the dynamics of invasive processes have generally resorted to one of three categories of models to explain invasion behavior, spread, and success. ***Nonspatial models*** are the simplest. In these, knowledge of the spatial locations of invading organisms is not known and the "contagious processes," such as transfer rates of individuals from one point to another, also are unknown. These models simply use projections derived from population demography, such as exponential or logistic growth equations, to predict changes in numbers of the invasive species through time. Spatially implicit models, discussed in Chapter 8, include spatially structured data, such as the correspondence between spatial variation in the environment and population growth, predicted in simple regression equations, to forecast rates of change in invasive populations as they encounter physical and ecological variation in a new environment. Spatially explicit models include spatial locations of invasive organisms and knowledge of "contagious processes" (site- or habitat-specific rates of movement, birth, or death, among others) to predict the rate and manner of invasive spread (Peters 2004).

Many invasions show behaviors that can be modeled as wave motions, in which individuals at a particular point move outward in concentric circles of ever-expanding radii. This view of biological invasion was recognized intuitively and described conceptually over 40 years ago, and is in fact a form of spatially explicit modeling. The British ecologist, Charles Elton, in his classic book, *The Ecology of Invasions by Animals and Plants* (Elton 1958), included maps with concentric lines depicting the spread of such introduced species as the European starling (*Sturnus vulgaris*), the muskrat (*Ondatra zibethica*), and the Chinese mitten crab (*Eriocheir sinensis*).

Before Elton's work, biometrician J. G. Skellam, in his classic paper *Random Dispersal in Theoretical Populations* (1951) described the spread of an invading organism as a type of ***reaction-diffusion model***. Such a model predicts that the advancing front of the organism should travel as a wave at a velocity (V) described as

$$V = 2\sqrt{rD}$$

where r is the population's intrinsic rate of increase and D is the ***diffusion coefficient***, equal to one-half the mean squared distance moved in a time unit by an organism (Godfray and Crawley 1998). For example, D is often expressed in km^2/year (e.g. Grosholz 1996). For all its simplicity, the predictions of this equation do match observed results well in many species (Grosholz 1996; Godfray and Crawley 1998). The speed of advancement in a muskrat invasion, for example, was locally constant, but influenced by topography and habitat preference (i.e. the muskrat's affinity for wetlands) (Skellam 1951). The model, however, can be modified to account for spatial heterogeneity and the patchy distribution of habitats by taking the form

$$V = 2\sqrt{r_a D_h}$$

where r_a is the arithmetic mean of the population's intrinsic growth rate across patches and D_h is the harmonic mean of the diffusion coefficient across patches (Shigesada et al. 1986). Both values can be calculated if one knows the rates of growth and spread in a sufficient number of habitat patches to calculate a reliable average. This model also has performed well when subjected to more stringent experimental tests in which the value of r was calculated from a life table and the value of D from controlled experiments of dispersal, then compared to data associated with an actual invasion. Andow et al. (1990) subjected the wave model to such tests with an invasion of muskrats, the cereal leaf beetle (*Oulema melanopa*, a European insect introduced in the US in 1958) and a butterfly (*Pieris rapae*, also European and introduced to the US several times in the nineteenth century). The model performed well for the muskrat and butterfly, but drastically underestimated the rate of spread in the beetle. Andow et al. (1990) believed that the model failed in the case of the beetle because it did not incorporate the effects of rare, long-distance dispersal by a few individuals. Such events, although uncommon, can profoundly affect the rate of spread. More sophisticated models attempt to incorporate such effects, along with effects of density dependence and carrying capacity as inner circles become saturated with individuals. For example, Veit and Lewis (1996) constructed a model with such elements to describe and explain the spread of the House Finch (*Carpodacus mexicanus*) from a small population of about 250 birds in New York to a population that now covers most of the United States. Their model predicted that range expansion would be slower than expected by traditional models due to Allee effects, but that speed of distribution would increase at an increasing rate as the population grew. Both of these predictions are confirmed in historical data. The model's incorporation of long-distance dispersal by a few individuals also matched well with the rather jagged and erratic pattern of historic expansion.

A problem with simple reaction-diffusion models is that, although the population density is allowed to vary across the landscape, the landscape itself is assumed to be spatially homogeneous, and the redistribution of invading individuals is assumed to occur as a random dispersal process. Further, dispersal and reproduction of the invading species is assumed to occur simultaneously and continuously. Sometimes, these conditions are, in fact, the case, but not always. Many invasive species, especially insects, tend to disperse in one life stage and reproduce in another. Further, many studies of invading organisms show that differences in landscape characteristics are not only present, but important to an invading organism, and, therefore, long-distance dispersal events, in which invaders "leapfrog" ecological and landscape barriers, although often rare, are nevertheless especially significant. One way to incorporate long-distance dispersal functions and stage-specific reproduction and dispersal in an invasive species is to switch from reaction-diffusion models to ***integrodifference equation* (IDE) *models***, which break dispersal and population growth into separate stages. An IDE model has two parts: a difference equation that describes population growth at each point in the landscape and an integral operator that accounts for the pattern of dispersal of organisms in space (the so-called "dispersal kernel"). Thus, all IDE models have the general form of

$$N_{t+1}(x) = \int_{\infty}^{\infty} \mathrm{k(x,y)f}[N_t(y)]dy$$

Where $N_{t+1}(x)$ is the population density at some destination point x, which is a function of the population growth at each source point y ($f[N_t(y)]$) and the movement of individuals from source point y to destination point x is a function of the shape of the dispersal kernel, k. Interestingly, IDE models reveal that it is the long-distance component of dispersal that ultimately governs invasive speed, even when long-distance dispersal is rare (With 2002). If not all life stages of an invasive species disperse (and this is true more often than not), models that lack the element of stage-structured dispersal, like reaction-diffusion models, will overestimate the speed of invasion.

IDE models are examples of ***stratified diffusion models*** in which elements such as long-distance dispersal and density-dependent rates of spread are incorporated more explicitly. In these models, populations at different distances from the source of invasion are assigned different values of r and D, thereby creating different layers or strata in the dispersing population. Thus, stratified diffusion models resemble age-structured models of population growth, except that the founding of each colony in successive strata takes the place of "birth" and colony growth takes the place of aging. If new colonies are established near existing colonies and coalesce, the rate of spread changes from accelerating to linear. This pattern of invasion has been referred to as "starburst" to distinguish it from the traditional "traveling wave" form. Godfray and Crawley (1998) note "Both types of spread (traveling wave and 'starburst') are seen as two ends of a single continuum; the key parameter is the distance between successive foci of establishment. When this distance is small, the assemblage behaves like a traveling wave, but when it is large starburst effects predominate."

The reaction-diffusion model has proven a useful paradigm in describing, explaining, and, in some cases, predicting patterns of movement associated with invasions of non-native species. However, other types of patterns exist, patterns in which factors other than population growth and diffusion coefficients are the controlling agents of spread. Landscape ecology also matters in biological invasions, as can be seen in models developed by With (1999) that examined species with differing dispersive abilities in landscapes with random, fragmented, and clumped habitat dispersion. With's models indicate that, in general, the potential for the spread of an invasive species is enhanced past a threshold level of landscape disturbance and fragmentation, but the absolute level of such a threshold is affected by characteristics of both the landscape and the invasive species. Once the disturbance threshold has been reached or exceeded, an invasive species will spread faster in more clumped, contiguous habitat than in more fragmented habitat (Figure 9.14), suggesting that when an invasive species has limited dispersive abilities and is at least somewhat of a habitat specialist, deliberate habitat fragmentation, although an idea anathema to traditional conservationists, could slow, or even halt, invasive spread at relatively low levels of landscape disturbance. For example, some management agencies, such as the US Forest Service, create "barrier zones" at invasion fronts of advancing gypsy moths (*Lymantria dispar*), a Eurasian species to North American in the late nineteenth century, whose larvae do great damage to many kinds of trees. In this case, Forest Service workers at the barrier zone employ direct suppression or eradication activities against the gypsy moth (Sharov and Liebhold 1998). However, the same strategy could be employed, in principle, by creating ecological or habitat barriers that a habitat-specialist invasive species with poor dispersive abilities could not cross (With 2002).

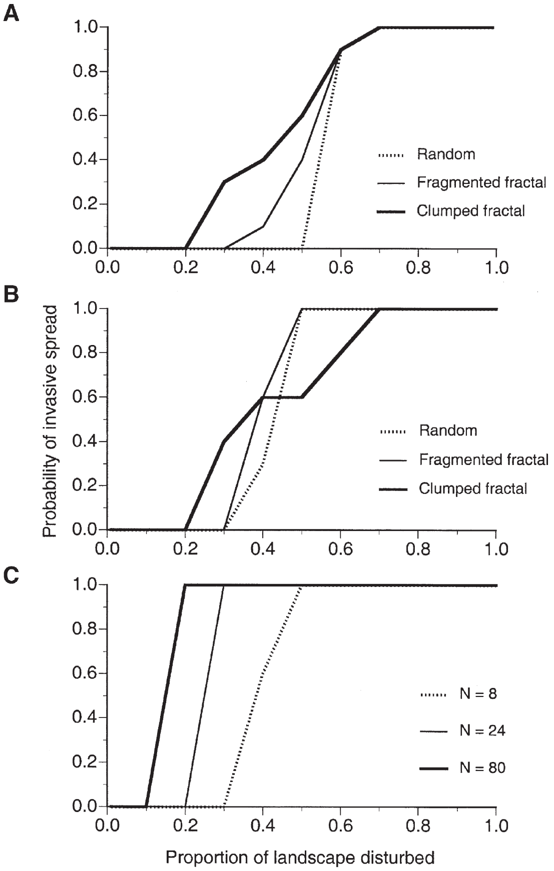

FIGURE 9.14. Probability of invasive spread as a function of landscape disturbance under conditions of randomly distributed, fragmented fractal, and clumped fractal habitat distribution. (A) An invasive species with poor dispersal ability (can disperse only to immediately adjacent (bordering) cells in the model landscape matrix, dispersal "neighborhood" of four cells) constrained to move only through adjacent cells of suitable habitat in different landscapes. (B) Invasive spread for a species with better dispersal ability (can disperse to adjacent and diagonal cells, dispersal neighborhood of eight cells) in different landscapes. (C) Invasive species that vary in dispersal ability (dispersal neighborhoods of 8, 24, and 80) in different landscapes. Note that, regardless of landscape pattern, probability of invasion reaches certainty ($P = 1.0$) if more than 50% of landscape is disturbed, even for species with poor dispersal abilities, and at much lower levels for species with high dispersal abilities. (With, The landscape ecology of invasive spread, *Conservation Biology*, Copyright 2002 by Blackwell Publishing.)

9.3.2. The Problem of Practical Response: How Do We Prevent or Control Invasions?

9.3.2.1. General Considerations

Although a few invasions by non-native species have proven beneficial, and many have been benign or at least inconspicuous, the enormous economic and ecologic damage done by some invasive species, as well as the direct extermination and endangerment of native species by non-native species throughout the world, suggests that further invasions of non-native species should be prevented. Thus, prudent management first should follow a strategy of preventing non-native species from entering. Recall from Figure 9.8 that individual invasive species typically enter predominately through a specific pathway. Therefore, the identification and monitoring of key pathways considered to pose the greatest risk of invasion, an approach known as ***pathway analysis*** or ***risk analysis***, represents a more systematic way in which conservation managers can more effectively focus limited resources on reducing the entry of invasive species. Using a pathway analysis approach, managers charged to control the introduction of non-native species would devise responses unique to particular pathways and to particular stages of invasion. For example, if entry already has occurred, managers should identify, control, and, if possible, eradicate non-native populations if they are established, especially when they are still small, and attempt to control their effects on native species if their populations become large, widespread, well-established, and beyond hope of eradication. Management strategies, therefore, change with the status of the invasive species.

One example of a response protocol conceptually grounded in a pathway analysis approach that specifies policy and management options, with specific recommendations, is that recommended by the Ecological Society of America (ESA) to US federal government agencies with responsibilities in preventing the introduction of alien species, or eradicating or controlling them once they have arrived (Lodge et al. 2006) (Figure 9.15). Within the flow of this figure, you can see that there are broad overall types of control strategies. One category consists of ***protectionist approaches*** that focus on preventing non-native species from entering the system, and emphasize monitoring and

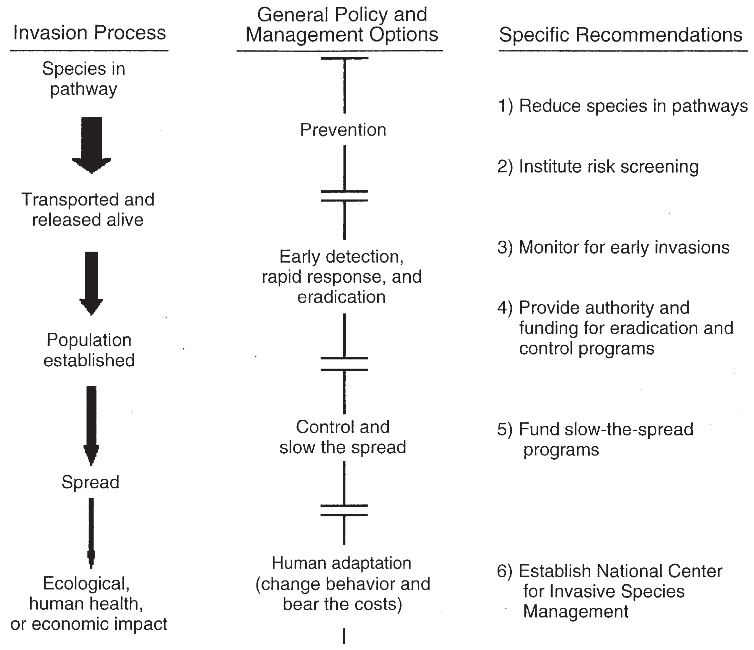

FIGURE 9.15. Stages common to all invasive species (left column), policy and management options appropriate to each stage of the invasion process (middle column), and specific management recommendations for responding to each stage of invasion (right column). In the left column, arrows decline in thickness at each level to indicate that the proportion of species that proceeds to each successive step decreases. However, because global trade and commerce are increasing, the number of species invasions is increasing with time. Recommendations in the right column correspond roughly to stages of invasion, but recommendation 6 should actually be considered a first step for any country to establish and support all other management options. (Based on recommendations developed by the Ecological Society of America for US federal agencies involved in preventing introduction of non-native species, or in their subsequent eradication or control. Lodge et al. 2006. Biological invasions: recommendations for U.S. policy and management and management. *Ecological Applications* 16:2035–2054. Reprinted by permission of the Ecological Society of America.)

surveillance at potential entry points to *prevent* the introduction of a non-native species. The second category consists of ***interventionist approaches*** that attempt to control, reduce, or even eradicate the invasive species once it has entered the system (Ashton and Mitchell 1989). In dealing with invasive plant species in particular, especially in aquatic environments, there are six types of interventionist control techniques that can be effective. These are: (1) manual removal, (2) mechanical control (using machines to mow, uproot, shred, or dredge out established plants), (3) chemical control (herbicides), (4) biological control (introduction of a specific parasite or predator to decimate the invader), (5) environmental manipulation (especially water level manipulation), and (6) the direct use of the invasive species for some economic benefit (i.e. harvest) (Ashton and Mitchell 1989). Despite the daunting prospect of trying to eradicate an established invasive species, some such programs have actually succeeded. One common feature of successful control programs is that the infestation was attacked early when the invasive species was low in numbers and small in extent. A second feature was that, in such successful efforts, the invasive species was confined to one location. Under these conditions, all of the above techniques have been effective. Even the much-maligned carp (in this case, the grass carp, *Ctenopharyngodon idella*), itself an invasive species, has been used successfully as an agent of biological control to eradicate non-native submerged plants (Ashton and Mitchell 1989).

Where invasive species have become well established, some attempts at control, and even eradication, have still been successful, but the range of effective techniques becomes more limited. Manual or mechanical removal is not practical when invasions become widespread. However, chemical and biological controls may still be effective. For example, an invasion of water hyacinth on Lake Hartbeespoort in The Republic of South Africa was eradicated with large scale use of herbicides (Figure 9.16a). An infestation of the water fern *Salvinia molesta* was eradicated on Lake Moondarra in Australia through the introduction of another non-native species, the Brazilian beetle or Salvinia weevil, *Cyrtobagous salviniae* (Figure 9.16b). In the case of the beetle, environmental conditions also played an important role, with drought reducing populations of *Salvinia molesta* to low levels just prior to the beetle's introduction.

The risks of biological control, especially of introducing a non-native biological control agent like a Brazilian beetle to an African lake, are many, but can be reduced where a native species can be used as the control agent. For example, to control the invasive aquatic weed, Eurasian watermilfoil, Sheldon and Creed (1995) evaluated the effects of a native North American aquatic weevil, *Euhrychiopsis lecontei*. In a controlled experiment, Sheldon and Creed compared the growth of Eurasian watermilfoil and ten native aquatic species within enclosures where weevils were present to those in which weevils were absent (Figure 9.17). By the end of the trial there was 50% less Eurasian milfoil in enclosures with weevils than in those without weevils, but weevils had no significant effect on any native species.

POINTS OF ENGAGEMENT – QUESTION 3

What elements of Sheldon and Creed's study eliminate or reduce risks associated with biological control? Does this study suggest protocols that could be applied to any consideration of using biological control as the means to manage an invasive species?

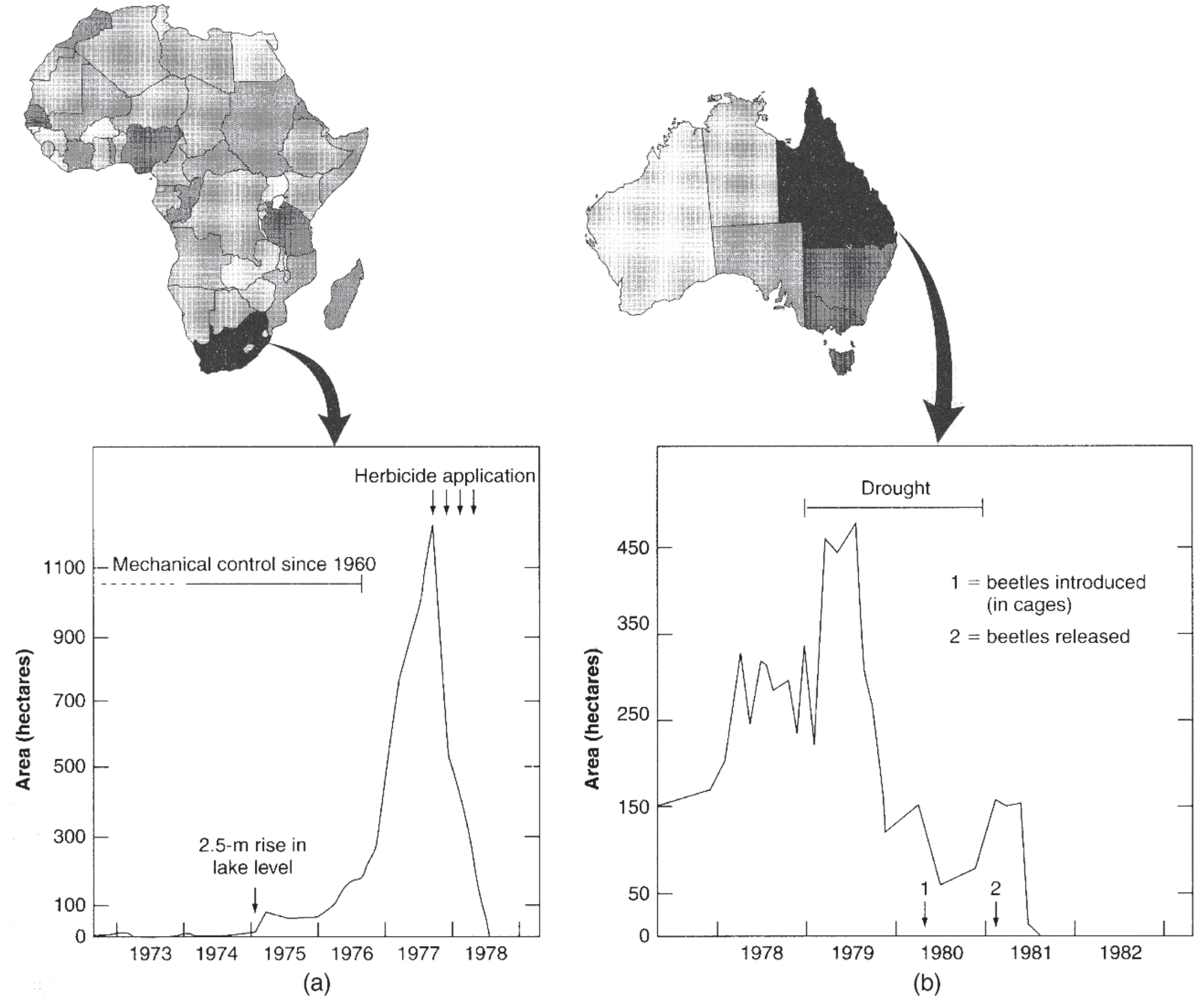

FIGURE 9.16. (a) Changes in the area covered by water hyacinth (*Eichornia crassipes*) on Lake Hartbeesport, Republic of South Africa, before and after herbicide application. (b) Changes in the area covered by water fern (*Salvinia molesta*) on Lake Moondarra, Queensland, Australia, before and after introduction of the Salvinia weevil (an herbivorous beetle), *Cyrtobagous salviniae*. (Adapted from Ashton and Mitchell 1989; Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

Non-native animal species tend to be much more difficult to control, much less eradicate. For example, despite decades of chemical treatments, such as rotenone poisoning, or environmental manipulation (water draw downs or complete drainage) to eradicate carp, such efforts have usually had only short term effect, if that, and usually have proved more effective at eliminating native species. The carp easily re-established themselves in most cases. The more desirable native species often did not. Mussels such as the Asian clam (*Corbula amurensis*), zebra mussel, and other invasive invertebrates have proven impossible to remove from aquatic environments once established, making preventionist approaches all the more important to maintaining the health of aquatic systems. Nevertheless, there is a logical sequence of measures managers can employ to reduce the effects of invasive species. We now examine that sequence and the logic behind it.

9.3.2.2. *Step One: Preventing Entry of Invasive Species*

To prevent the initial entry of non-native species, managers should answer the following questions: (1) To what non-native species is my preserve, community or ecosystem most vulnerable? (2) Which of these non-native species has the greatest potential or opportunity to invade, based on its current distribution and pattern of dispersal? (3) What are the most likely points and methods of entry? Can these be closed or

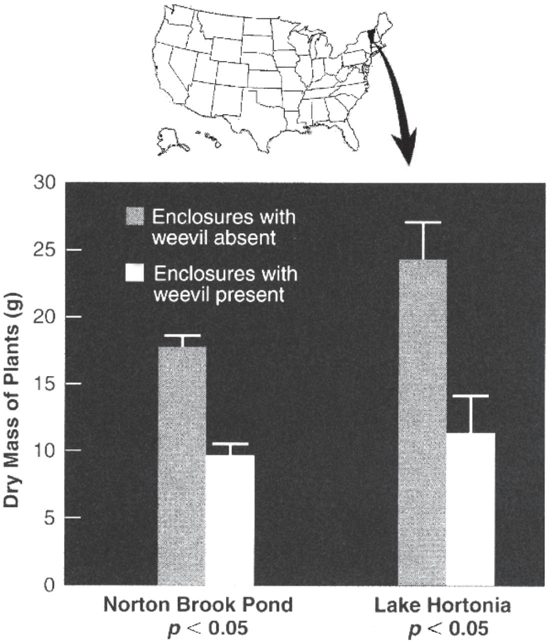

FIGURE 9.17. The effect of herbivory by the native North American aquatic weevil, the milfoil weevil (*Euhrychiopsis lecontei*) on Eurasian watermilfoil (*Myriophyllum spicatum*) in two Vermont (USA) lakes. Watermilfoil biomass is significantly lower where the weevil is present. (After Sheldon and Creed 1995. Fred Van Dyke, *Conservation Biology*: *Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

monitored in such a way as to prevent the entry of the non-native species?

Answering the first two questions requires a thorough knowledge of both the system being protected and the ecology of invaders that would be most adept at becoming established in it. Thus, conservation biologists must remain well-informed about current invasive species and their present distribution. In aquatic systems, unmanaged human disturbance and disruption of systems seems to increase the success of invaders. In the previously cited work of Moyle and Light (1996) on fish communities, the authors note that "In aquatic systems with high levels of human disturbance, a much wider range of species can invade than in systems with low levels of human disturbance" and "successful invasions in aquatic systems are most likely to occur when native assemblages of organisms have been temporarily disrupted or depleted." For plants, more disturbed communities tend to be more invasible than closed, less disturbed communities (Crawley 1987). Godfray and Crawley (1998) formalize this trend as a rule. Namely, "the rate of establishment of alien species will be proportional to the frequency and intensity of disturbance of the habitat." Further, in areas of disturbance, species are more likely to be transported by humans into other places. Thus, management actions that reduce human disturbance to the habitat reduce its invasibility and its rate of transmission of its own organisms into non-native habitats.

A correct answer to the third question can, in some cases, lead to intelligent and strategic efforts to control entry into the protected system by intensive monitoring at key points, or by changing the practices of persons, vehicles, or vessels moving through such points. It is not surprising that alien species richness is positively correlated with proximity to centers of human transport (docks, cities, railways, roads, trails) and inversely related to a habitat's degree of isolation (Godfray and Crawley 1998). In fact, although human activities often cause the extinction of native species, their activities establish new species at a faster pace in some taxa, such as plants, leading to an overall increase in local and regional biodiversity. Using databases covering the contiguous (lower) 48 states of the US, Michael McKinney determined that net plant diversity increased directly with human population density (Figure 9.18a), but, as the number of state non-native plant species increased, so did the number of native extinct and threatened plants (Figure 9.18b), suggesting competitive displacement of native species by non-native species (McKinney 2002). Overall plant diversity increased because gains of non-native species outpaced losses of native species. However, if a goal of conservation biology is to preserve threatened species, this is not good news, and the wrong way to increase local and regional plant biodiversity.

The correlation between human population centers and increased densities of alien species suggests obvious procedures that could lower the transmission and invasion of alien species, although all would be challenging to enforce. For example, changes in disposal and treatment of ballast water from foreign sources would, if implemented, achieve significant reductions in invasion rates of aquatic organisms throughout the world. At a regional level, cleaning and inspection of boat surfaces, and stringent removals of biotic material from boats, especially aquatic plants, entering and leaving vulnerable bodies of water also would reduce invasion probability. Although such an effort might be overwhelming from an enforcement perspective, it could succeed through voluntary cooperation achieved via public education. In terrestrial environments, seeds and spores of invaders are often carried on tires of autos or on the shoes or clothing of hikers. Road and trail closures in strategic areas can thus reduce the probability of invasion. Despite all these precautions, many invasions have been the result of escapes from cultivation or captivity, while others continue to occur because of intentional introductions. For example, introductions of non-native sport fish species are often performed at the behest of anglers, and even conservation managers (who ought to know better) sometimes plant non-native species along roadsides for beautification, cover, or food for wildlife because non-native species are often easier to plant and more cheaply obtained than native

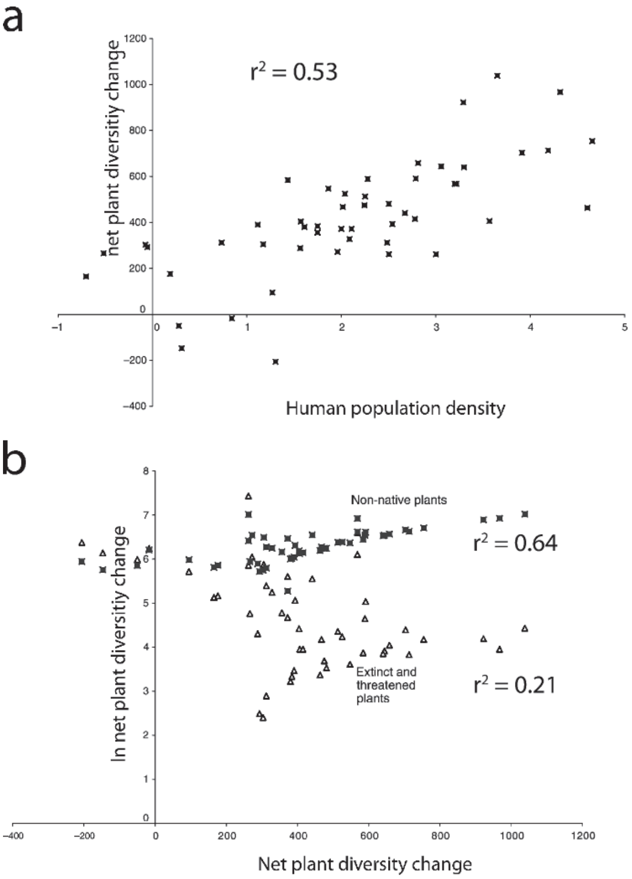

FIGURE 9.18. (**a**) Net plant diversity (species richness) gain in 48 contiguous US states is positively correlated to human population density. The horizontal axis displays the natural logarithm of human population density. The vertical axis is the arithmetic value of net species diversity change, equal to the number of established non-native species – threatened or extinct native species. (**b**) Numbers of non-native plants and extinct and threatened plants associated with different values of net plant diversity change. Net plant diversity gain in 48 contiguous US states is correlated with both increasing numbers of non-native plants and increasing numbers of extinct and threatened native plants. The horizontal axis is the arithmetic value of net plant diversity change; the vertical axis is the natural logarithm (ln) of the same value. (McKinney, Do human activities raise species richness? Contrasting patterns in United States plants and fishes. *Global Ecology and Biogeography*. Copyright 2002 by Blackwell Publishing.)

species. The long-term solution to these kinds of problems include: (1) more stringent controls on the importation and planting of non-native plants as ornamentals, and on the keeping, sale and distribution of exotic animals for pets, display or commercial use, (2) laws that require planting of native vegetation on public lands and right-of-ways and prohibit the planting of non-native species, and (3) more careful monitoring and quality control on seed mixes of "native" plant species, which sometimes inadvertently contain seeds of non-native species.

9.3.2.3. Step Two: Controlling Initial Infestations of Invasive Species

Small populations of invasive species are the easiest to control, and potentially can be completely eradicated. However, such small populations are also the most difficult to detect. Regular inventories of protected systems, with intentional and focused effort to detect non-native species considered most likely to enter the system, are essential to discover populations of alien species while such populations are still small, dispersed, and not well established. Once detected, strenuous efforts to reduce or eradicate such small populations are the best investments of management effort rather than delaying action until populations have grown too large.

There are several methods of eradicating small populations of non-native species. The most direct, and potentially most effective, is direct physical removal. Because sexually reproducing animal populations are limited by the number of females, killing or removing all females will eradicate an animal population. In plants, physical removal may require pulling up or cutting down every individual. Direct removal methods are effective if the invaders are few and confined to a small number of specific locations. However, direct removal is labor intensive and, therefore, often expensive.

In plants, some invertebrates, and some small mammals, a less labor intensive method of direct removal is chemical control, the application of pesticides. Pesticides, properly applied, can remove invasive species, and they are often the best choice, when the population of invaders is still small, because they can achieve complete eradication in some cases. However, the window of opportunity is narrow, and pesticides present significant risks under any conditions. Most pesticides are not species specific. They can kill individuals of native, non-targeted species, spread out of the target zone via air and water into non-target areas, and some can persist in the environment for an extended length of time, posing a longer-term threat to native species even after the alien species is removed. In plants, some herbicides may enter nutrient cycling pathways and be spread throughout the system, killing individuals of some species directly and interfering with nutrient uptake or metabolic pathways in others. Thus, pesticides and herbicides should not be used where they pose a potential threat to native, small or declining populations.

The alternative to chemical control is biological control, the introduction of a new species for the specific purpose of controlling, often through predation or parasitism, the alien invader. There are cases in which biological control successfully reduces, or even eliminates, the targeted invasive species. But there are also many failures, and there are always risks. The greatest risk is that of unforeseen effect and unintended consequence. Biological control usually requires the introduction of yet

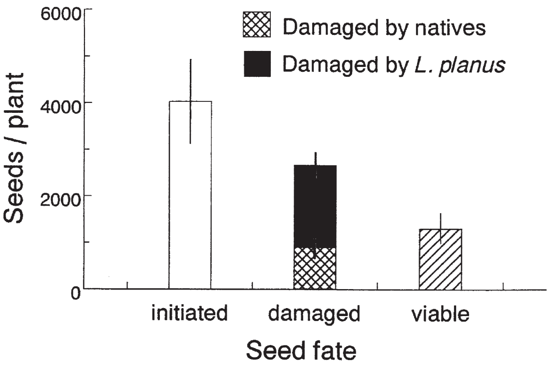

FIGURE 9.19. Seed reproductive effort and seed fate in a stand of Tracy's thistle (*Cirsium undulatum* var. *tracyi*) in Colorado, USA, July 2000. Note that the introduced European weevil, *Larinus planus*, damaged more seeds than all species of native insects combined, resulting in only one-third of seeds produced remaining viable for new reproduction. (Louda and O'Brien Unexpected ecological effects of distributing the exotic weevil, *Larinus planus* (F.), for the biological control of Canada thistle. *Conservation Biology*. Copyright 2002 by Blackwell Publishing.)

another non-native species to control the first non-native species. Like the old lady in the children's song who swallowed a fly, and then swallowed a spider to catch it, attempts at biological control can set in motion a chain of events that can rapidly escape management constraints, usually with very negative consequences. Mongoose (*Herpestes* spp.) introduced in Hawaii and Caribbean islands to control rats have proven themselves much more efficient at devastating populations of native island birds and reptiles, particularly ground-foraging skinks (a type of lizard, Family Scincidae) and snakes (Whittaker 1998). Two Eurasian weevils, *Rhinocyllus conicus* and *Larinus planus*, both introduced into the United States to control the spread of exotic species of thistles (*Carduus* spp. and *Cirsium arvense*), have had little effect on their target exotics, but have done considerable damage to native thistles, including endemic species with limited ranges like the Platte thistle (*Cirsium canescens*) and Tracy's thistle (*C. undulatum* var. *tracyi*). In one study, investigators found that *Larinus planus* damaged 74–100% of all terminal flower heads in sampled stands of Tracy's thistle, and reduced the seed production in damaged flower heads by 87–99% (Louda and O'Brien 2002). In sampled stands, *L. planus* damaged more seeds of Tracy's thistle than all other native insects combined, and, when added to damage from native insects, destroyed two-thirds of initiated seeds, leaving only one third of seeds produced as viable (Figure 9.19) (Louda and O'Brien 2002).

Using biological control usually concedes that the original non-native species cannot be eradicated, only limited. Predators and parasites may reduce the abundance or a prey or host species, but they rarely eliminate it, especially if the prey or host species is well established at high densities. Although chemical control carries its own array of risks, it is, in the end, almost always preferable to the risks of biological control.

9.3.2.4. Step Three: Controlling Negative Effects of Invasive Species on Native Populations

Throughout the world, many invasive species are now so well-established that their eradication in the new environment is no longer a realistic goal. It is highly unlikely, for example, that the introduced Eurasian cheatgrass will be eliminated from western range communities in the United States by any amount of management effort, or that starlings will cease to be an abundant species among North American birds in the foreseeable future. Rather than commit further resources to futile efforts at eradication, managers and conservationists should be determine in what ways the distribution and abundance of non-native species can be reduced and how their negative effects on native species can be mitigated. In grasslands, many introduced species, such as cheatgrass, can withstand heavy grazing better than native species. Managing grazing levels to create conditions that favor natives over exotics does not eliminate introduced species, but can shift community distribution in favor of natives. In aquatic communities, alteration of water levels and flow rates can be used in ways that favor native plants and animals over invaders. In forest ecosystems, harvesting practices and methods can create environments that favor native species over introduced ones.

When eradication is no longer possible, managers and conservationists must accept the alien species as part of the community and determine what interactions they may have with other species and with the physical environment, and what resources they offer that could provide specific benefit and value. If such interactions and resources can be correctly identified, properly managed, and prudently used, positive features and components of the natural community can be conserved even in the presence of infestations of the invasive species. However, invasive species often completely eradicate similar, native species during the course of their invasion. Is it possible to restore native species once the invasive species has entered the ecosystem?

9.3.3. The Problem of Restoration: Can Native Populations Eradicated by Invaders Be Restored? The Case of the White-Clawed Crayfish

The white-clawed crayfish (*Austropotamobius pallipes*) (Figure 9.20) is a native European freshwater crayfish once common throughout Europe. Today the species finds itself on the Red List of Threatened Animals of the International Union for the Conservation of Nature, designated as a "vulnerable species." The white-clawed crayfish did not used to be "vulnerable," but it is now because of the increasing invasion of the North-American red-swamp

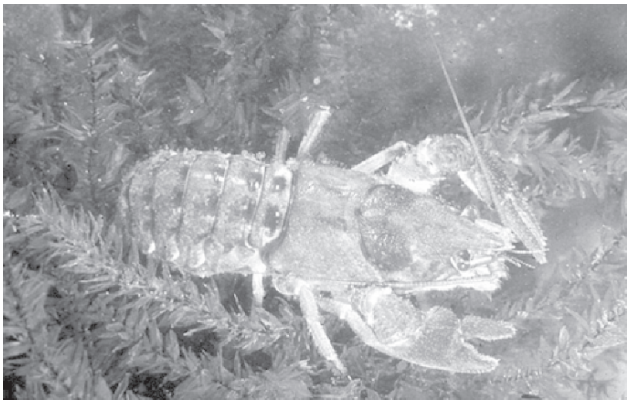

Figure 9.20. The white-clawed crayfish (*Austropotamobius pallipes*), a species of native European crayfish now endangered by introductions of the North American red-swamp crayfish (*Procambarus clarkia*) and fungal disease associated with this species. (Photo copyright Environmental Agency (England and Wales))

crayfish, *Procambarus clarkia*. The red-swamp crayfish has been highly successful in Europe, rapidly expanding its range and proving a superior competitor relative to the white-clawed crayfish and other native European crayfish species. The red-swamp crayfish also is aided in its expansion by a weapon even more powerful than its competitive abilities. It is a vector of "crayfish plague," also known as aphanomycosis, or, perhaps best put by the French, "la peste,"a lethal disease caused by the oomycete fungus *Aphanomyces astaci*. North American populations like the red-swamp crayfish may be highly infected (some estimates put the infection rate as high as 50% in some populations), but are relatively resistant to it. European crayfish, on the other hand, are not. Fungal hyphae (filaments) grow from spores that attach to the crayfish that can penetrate and grow in the soft parts of the cuticle of its exoskeleton. The fungus also attacks nervous tissue, including major nerve cords. Thus, infected crayfish often lose coordination, fall over on their backs and cannot right themselves, and become active during daylight hours (crayfish are normally nocturnal), increasing their risk of predation. They may die within 2–3 weeks of exposure, and the first sign of the presence of the disease may, sadly, be the presence of many dead crayfish in a river or stream. Armed with both this disease agent and strong competitive abilities, the red-swamp crayfish has decimated many populations of white-clawed crayfish. Although the first introductions occurred nearly 150 years ago in Lombardy, Italy, the red-swamp crayfish has spread much faster throughout the rest of Europe in recent years because it is aided by yet another asset, human distribution and preference. Since the 1960s, the red-swamp crayfish has become the preferred species for commercial crayfish farming operations, and, from these, it is increasingly spread throughout Europe as both human food and fish bait.

The southernmost limit of *A. pallipes* is the southeastern mountains of Spain, but this species has been decimated here as elsewhere, although losses have been more recent. During the 1980s, 90% of the rivers in southeast Spain lost their native crayfish populations. Today the white-clawed crayfish remains only in isolated, remote headwater areas where *P. clarkia* is absent because of ecological barriers.

Jose Maria Gil-Sánchez and Javier Alba-Tercedor of Spain's University of Granada, both of whom have investigated the ecology and conservation of this native crayfish for many years, initiated a study to examine the specific causes of extinction of the remaining populations of the white-clawed crayfish in southeast Spain, to determine the importance and role of habitat isolation for the conservation of this species, and to implement and assess a restocking strategy designed to restore the white-clawed crayfish to streams from which it was now absent (Gil-Sánchez and Alba-Tercedor 2006). From the outset, the local news for this study was bad. Of 26 native crayfish populations present in the study area in 1991, only 14 remained by 2002. Not only was this population loss (46%) severe, but 64% of the stream lengths occupied by native crayfish in 1991 also had been lost during the same period (Figure 9.21). With an extinction rate of over one population per year, total extinction was expected between 2015 and 2021 (Gil-Sánchez and Alba-Tercedor 2006). Causes of extinction varied, but the most common agent was the displacement of the white-clawed crayfish by the red-swamp. Drought and disease accounted for the rest of known extinctions.

In examining stream traits, Gil-Sánchez and Alba-Tercedor found that some form of physical or ecological barrier was present in 100% of the remaining occupied streams, and streams with surviving populations were those farthest from the nearest populations of red-swamp crayfish. However, physical or ecological barriers also were present in 82% of streams where extinctions occurred. Although this is a statistically significant difference, it means, at a biological level, that such barriers were no guarantee of persistence for native crayfish. Although these barriers might stop movements of red-swamp crayfish into the stream, they probably could not stop dispersal of the crayfish plague, which can be transmitted by things other than crayfish, including wet boots and fishing tackle. This perspective was supported by the fact population survival rates were highest in streams that were farthest from villages, paved roads, and unpaved roads, and in areas with the least amount of cultivated land (Gil-Sánchez and Alba-Tercedor 2006).

Although some populations were victims of the invading species, disease, or drought, others appeared to have been victims of demographic stochasticity. As we have noted earlier, small populations are vulnerable to random population fluctuations that, while having little or no effect on large populations, can lead to the complete extinction of a small one. As Gil-Sánchez and Alba-Tercedor astutely noted, “It appears that the last period which registered the highest extinction rates (since 1998) was a typical case of environmental stochasticity with random catastrophes.… So, unfortunately new extinctions may be expected …” (Gil-Sánchez and Alba-Tercedor 2006:120).

Gil-Sánchez and Alba-Tercedor identified 25 stream areas for potential restocking sites, ultimately selecting 11. They also made three trial stockings in streams already occupied by red-swamp crayfish. In these latter instances, all native crayfish died within 3 months, all of the victims showing hyphae (fungal infections) similar to *Aphanomyces astaci*. Six survival trials from the remaining 11 were frustrated within 6 months by floods or human disturbance, although some of these could be used for experimental monitoring for varying lengths of time (Figure 9.22). Only five stream areas maintained original habitat quality for the entire study period (5 years). Of these, restocking was successful in two stretches. In these, Gil-Sánchez and Alba-Tercedor noted that not only did re-introduced white-clawed crayfish survive, they also expanded their range along the length of the stream by 300–1,000 m.

Many of the results of this study are discouraging. As Gil-Sánchez and Alba-Tercedor admitted, “The present data show that the native crayfish of the south-eastern mountains of Spain have a high probability of becoming extinct soon” (Gil-Sánchez and Alba-Tercedor 2006:118). The 11 streams selected for stocking suffered a variety of unforeseen, and often unmanageable, problems, knocking out over half of the selected restocking habitat less than 6 months after the re-stocking effort began. But, in five stable and undisturbed streams, restocking efforts in two (40%) were successful. Thus, Gil-Sánchez and Alba-Tercedor could state that, in their study area, “it was possible to recover the lost habitats, where *P. clarkii* was still absent through ecological barriers. Restocked crayfish showed good adaptation and fast expansion resulting in good breeding success related to habitat quality” (Gil-Sánchez and Alba-Tercedor 2006:120).

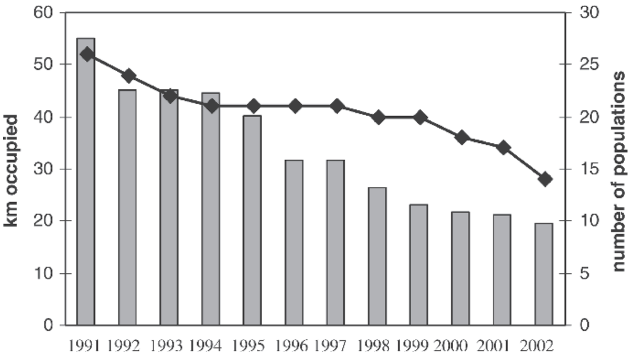

FIGURE 9.21. Decline of white-clawed crayfish (*Austropotamobius pallipes*) populations in southeastern Spain following introduction of the North American red-swamp crayfish (*Procambarus clarkii*) between 1991 and 2002. Line represents the number of populations and bars represent occupied habitat size. (Gil-Sánchez and Alba-Tercedor 2006. Copyright 2006 by Springer-Verlag, New York, Inc. With the kind permission of Springer Science and Business Media.)

Despite many setbacks and frustrations, the results provided warranted optimism, and the authors’ valuable insights are worth quoting at length.

> *The present data showed that it was possible to avoid extinction of the native crayfish, within a short time scale. However, it must be based on an urgent management strategy, since isolation as a strategy is not a guarantee sufficient for their conservation, considering the fast extinction rate. The best conservation strategy should be to obtain as high a number of populations as possible, since the risk of extinction of each population is mainly affected by stochastic factors, with almost no chance of prevention through management. However, loss of populations from habitats in headwater areas can easily be recovered. It is logistically easy to restock by translocations within suitable habitats previously tested by survival trials. The two new restocked populations diminished the last extinction rate (since 1998) from 1.5 populations/year to 1.0 population/year. Therefore, annual extinction rates can be buffered by this type of management within up to 30 brooks or streams. These new populations will be affected by the observed stochasticity of extinction probability, but the stocking/restocking program represents the best chance for the future of the crayfish.*
>
> (Gil-Sánchez and Alba-Tercedor 2006:120)

Although there are endangered species that have been restored to the wild, the case of the white-clawed crayfish

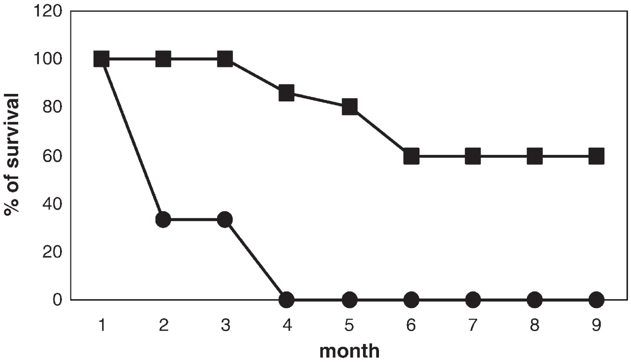

FIGURE 9.22. Survival curves for field survival trials of the white-clawed crayfish (*Austropotamobius pallipes*) in streams in southeastern Spain. Circles indicate survival trials carried out within streams with established populations of the non-native invasive red-swamp crayfish (*Procambarus clarkii*) ($n=3$). Squares represent survival trials carried out within potential habitats for recovering white-clawed crayfish populations where red-swamp crayfish were not present ($n=7$). (Gil-Sánchez and Alba-Tercedor. Copyright 2006 by Springer-Verlag, New York, Inc. With the kind permission of Springer Science and Business Media.)

is one of the clearest cases of a population that was restored following decimation by an alien species and its associated disease. The "urgent response" approach of the conservation scientists involved, the correct identification of a key variable needed for population persistence (in this case, isolation), and the careful selection and monitoring of potential restocking sites provide an excellent example of how one might approach a similar situation. At the same time, the study also reveals, thanks to the thoroughness and candor of the investigators, the high levels of risk, uncertainly and potential failure that could accompany a conservation restocking program designed to restore a native species displaced by a non-native competitor.

9.4. Practical Steps in Making Management Decisions for Populations: A Conceptual Framework

Conservation biology has traditionally suffered in its treatment of small populations because of tension between two relevant paradigms, the ***small population paradigm*** and the declining population paradigm (Caughley and Gunn 1996). The small population paradigm provides theoretical insights into what makes populations small and keeps them small. Although it addresses particular dangers – genetic, demographic, environmental, and catastrophic – to which small populations are uniquely susceptible, the small population paradigm does not always illuminate what caused the population to decline and what ought to be done to restore it to viable levels.

The ***declining population paradigm*** originated in the applied sciences, and it is helpful in identifying the causes of species decline and their remedies. When applied in conjunction with theories from the small population paradigm, it can offer constructive insight for strategies that may lead to a population's recovery. What follows is a possible conceptual approach to managing a small population for recovery to viable levels.

Step One: Determine the Cause of the Decline – Populations may decline for many reasons. In conservation as in medicine, a correct remedy is impossible without correct diagnosis. The cause of decline may appear obvious, but the "obvious" cause may, in fact, have little to do with the observed decline. To determine the real reason for the population's decline, one should examine available data that compare the population in its present state with the same population in the past, particularly if records exist that describe the population when it was larger. Comparisons should focus on critical variables of interest:

1. *Geographic range* – What are the differences between the past and present geographic ranges?
2. *Habitat use* – What are the differences between past and present habitat use?
3. *Competitors, predators, parasites, and disease* – Are there differences in the types, species, or intensities of competitors, predators, parasites, or disease that interact with this population now compared to interactions of the past?
4. *Environmental conditions* – Are environmental conditions for the population today the same as or different from those faced by this population in the past?
5. *Integrative comparisons* – If data are available to answer the above questions, they can be integrated to answer more complex questions. An exhaustive listing of these is beyond the scope of this chapter, but some of the more important questions are:

    (a) How do distributions of competitors, predators, parasites, and disease organisms compare with present and historic distributions of the population? Are there obvious overlaps or disjunctions in particular interactions?
    (b) How has the availability of preferred habitat changed in the population's geographic range over time?
    (c) Are changes in range and habitat use, if any, associated with changes in environmental conditions experienced by the population?

    In addition to comparisons to historic conditions, an examination of present conditions should determine the status of two forces that, if present, must be stopped immediately if the population is to survive.

6. *Direct exploitation* – Does the population experience any form of direct exploitation by humans today, legally or illegally?
7. *Habitat destruction* – Is the critical habitat of the population, especially breeding habitat, stable in quantity and quality?

Important factors regarding present conditions – Historical data are not always available and, if they are, there are dimensions of a population's current status that merit examination independent of historic analysis. These are categories that can be examined in some detail through PVA simulation models, but they are repeated here because they can be examined through other kinds of analyses as well.

1. *Environmental stochasticity* – What level of environmental variation is present and does it affect population numbers?
2. *Demographic stochasticity* – What is the current status of the population's demography (birth rates, death rates, age-specific survivorship, mortality and reproduction, and immigration and emigration)?
3. *Genetic constraints* – What is the population's current level of inbreeding and heterozygosity? Does the population show any obvious signs or effects of inbreeding, including morphological distinctives, deformities, sterility, or abnormal juvenile mortality?

4. *Susceptibility to natural catastrophes* – Is the population currently susceptible to any types of natural disasters? If so, what kind, and at what frequency and severity? Is it feasible to protect the population from such disasters?

Step Two: Formulate a Hypothesis About the Cause of Population Decline – Even after a careful examination of all available data (which will be imprecise at best and absent at worst), the facts alone will not unequivocally reveal the cause of the population's decline and its persistent low numbers, nor will they necessarily offer an obvious management solution. To advance further, one must make the most informed guess possible about the cause of the population decline, and frame this guess as an explicit hypothesis. For example, as was the case with the Lord Howe Island woodhen, examination of historical comparisons on numbers and distributions, combined with an examination of the distributions and numbers of predatory species, led to the conclusion that predation and nest and habitat destruction by pigs were the most important agents of population decline. This idea could then be framed more rigorously as a research hypothesis: "The distribution of Lord Howe Island woodhens is limited by pigs."

This hypothesis leads to a specific prediction: if pigs are eradicated from the island, woodhens should expand their range and habitat use. Where possible and appropriate, the prediction could be framed as an experiment with appropriate control and replication – areas accessible to woodhens that contained pigs and other, similar areas of equal accessibility from which pigs were removed. A significant increase in woodhen distribution and abundance in pig-free areas would support the hypothesis. No difference between pig-free and pig-infested areas would negate the hypothesis and lead to formulation of a new hypothesis with appropriately different predictions and experimental design. The hypothesis and its predictions should be subsequently incorporated into management actions. In the case of the Lord Howe Island woodhen, the appropriate management action was a pig eradication program, a practical, albeit labor-intensive effort that had the potential for effective implementation and success.

Step Three: Determine Potential Avenues for Increasing Population Size – Whether experimental manipulation is possible or not, whether the results of such experiments are clear or not, managers will have to try something to lead the endangered population toward recovery. Ultimately, management actions to increase the size and persistence of small populations fall into one of three categories:

1. *Intensive ecological and environmental management of the species in its natural habitat*. Using this strategy, managers depend primarily on natural reproductive capabilities and adaptations for survivorship of a wild population, but enhance the environment in such a way as to maximize favorable environmental conditions, minimize detrimental environmental variation, and optimize population demography toward maximum growth through removing competitors, predators, and parasites; controlling disease; creating favorable habitat; increasing the quality of available habitat; improving opportunity for migration and movement, and, in some cases, translocating animals and offering supplemental feeding. In terms of habitat enhancement, this kind of effort has been more formally described as the ***optimal niche gestalt*** approach to habitat management. The optimal niche gestalt strategy invokes the idea that there are structural features of an environment that allow a species to thrive over and above those that allow it to merely persist (James et al. 2001). Thus, managers should first identify these features by identifying correlations between environmental features and high-density populations or subpopulations, experimentally test hypotheses about the underlying causes that lead to these correlations, and then, informed by the results, manage selected sites intensively so as to favor processes and structures that create the features associated with these high density populations rather than simply managing to create average environmental conditions found over the species range (James et al. 2001).
2. *Supplementing wild populations through additions of captive-reared individuals* – To employ this strategy, managers must have or create a captive-bred population, the offspring of which they release into the wild at favorable sites to supplement existing populations or start new ones. Without such additions, the Lord Howe Island woodhen population might have perished. However, managers must first ask astute questions to evaluate the risks associated with supplemental additions from captive stock and determine if such a strategy is wise. Captive-bred individuals often have low rates of survivorship and fecundity in natural environments. Captive breeding increases the opportunity for inbreeding, and the release of highly inbred individuals into the wild population may perpetuate unfavorable genetic traits. Inbred individuals may carry an "opportunity cost" to the population by mating with healthy wild individuals, reducing reproductive success and removing opportunities for mating by unrelated individuals. Even if not inbred, captive-reared individuals may be genetically different from wild populations. These differences may spread traits that are not environmentally adaptive, or that genetically contaminate the population as a true phylogenetic species. Finally, if a captive-bred population does not already exist, the decision to start one means that some individuals must be taken from the wild population to do it. Animal capture and handling is risky even under the best of conditions. Some animals will die from trapping, handling, or transport. Some will not survive in a captive environment. Thus, the wild population will be rendered even smaller and more prone to extinction.

3. *Removal of all remaining wild individuals to preserve the population in captivity* – This scenario is the most extreme, but not hypothetical. Faced with an extremely small number of individuals in the wild, the US Fish and Wildlife Service captured all remaining California condors and vested all efforts for the survival of this species into captive-breeding programs in Los Angeles and San Diego (California) zoos, with the hope that, one day, condors could be re-established in the wild from captive-reared birds. Individuals of the last wild population of black-footed ferrets were captured in Wyoming and placed in a captive-breeding program just before canine distemper eliminated the wild population. Black-footed ferret populations have been re-established in Wyoming, Montana, Utah, Colorado, South Dakota, and Arizona using captive-bred individuals, and condors are beginning to be re-established in California.

Managers must assess which strategy carries the greatest potential for recovery and the lowest risk of loss. Unfortunately, those may be two different strategies. Small populations leave little room for error, and the price of failure is often extinction. Managers must examine data carefully, formulate clear hypotheses regarding causes of population decline, and make testable predictions that can be evaluated in management actions if they are to be effective in managing small and declining populations.

9.5. Synthesis

The theories of population viability analysis addressed in Chapter 8 are complex. The problems faced by real endangered populations, such as those we have examined in this chapter, can be even more bewildering. The application of PVA to real populations often reveals that: (1) assumptions about the population's demography are incorrect; (2) what we do not know is more important than what we do know, and therefore more research is required, but (3) the projected decline of the population, whether woodhens, crayfish, or perennial shrubs, may not allow time to investigate what we do not understand. We are left in the classic conundrum of conservation, the "ready, fire, aim" syndrome that requires management action not fully informed by demographic understanding. Thus, a manager's personal virtues of insight, perseverance, and determination in restoring an endangered species may loom larger than his immediate scientific knowledge.

That said, we also must recognize that, as conservation biology matures as a science, it will increasingly rely upon generally tested principles of population management that apply to common and rare species alike. Careful experimental design, systematic experimental approaches like trend analysis and factor resolution, and long-term population and ecosystem studies will, in the long run, make management responses to conservation crises of imminent extinction more intelligent and informed, and perhaps even lead to fewer crises. Yet the importance of insight and perseverance will remain.

Even as scientific insight is sharpened by careful investigation, population restoration requires social, political, and legal constructs to ensure success. The return of the gray wolf in the north central region of the United States is less a triumph of science than a radical shift in human culture, from one that once persecuted this species to one that now admires and protects it. Each time such a transformation takes place in the human perception, the restoration of an endangered species is a more hopeful project.

But humans can be agents of endangerment as well as solutions to it. Not only is the human population increasing, but its increasingly global commerce and transportation systems can threaten and even eradicate native plants and animals through the introduction of non-native invasive species. We can, perhaps, manage and mitigate some of the harm done by these unplanned introductions, but much harm is also done by the introductions we accomplish with planning and intention because humans continue to intentionally introduce species. We will be better conservationists when we commit to no longer intentionally introducing species anywhere, for any reason, under any circumstances.

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10

The Conservation of Habitat and Landscape

Conservation is a geographic problem because one of the greatest threats to biodiversity is habitat loss and fragmentation.

Scott M. Pearson 2002

In this chapter you will learn:

1. **Concepts and definitions of habitat and landscape and the role of habitat conservation in conservation biology**
2. **Definitions of habitat heterogeneity and patch dynamics**
3. **Specific mechanisms through which habitat loss, fragmentation, and isolation threaten biodiversity**
4. **Principles of reserve design and their role in habitat conservation**
5. **Means of reducing the impacts of human disturbance to conserve habitat and habitat-dependent populations in non-reserve environments**

10.1. The Definition, Concept, and Importance of Habitat

10.1.1. What is Habitat?

Habitat can be defined as *the physical and biological surroundings of an organism* (Bolen and Robinson 1995) or, more precisely, as sites having appropriate levels of the biotic and abiotic features required by a species for survival and reproduction (Pearson 2002). That is, habitats are arrangements of resources that meet the needs of individual species. Although we often "name" habitats according to the dominant vegetation present in them (for example, "sagebrush habitat," "grassland habitat," or "forest habitat") we should recognize from the outset that the *vegetation communities* we might use to label habitats are not the same as the habitat itself, although they may be associated with it. Habitats are usually conceived as occurring in ***patches***, which can be defined as contiguous regions of the same kind of habitat (Pearson 2002) or as *sites where the habitat conditions of a species are realized*. Patches often exist in networks in which a *collection of spatially distinct patches is connected by linear elements* (structural definition) and *linked by a flow of individuals from patch to patch* (functional definition) (Opdam 2002:318). If this is what we mean by "habitat," what do we mean by "landscape?"

At regional or geographic scales, ***landscapes*** can be defined as *large areas* (measured at spatial scales of km^2 or higher) *that comprise more than one type of habitat distributed in numerous patches* (Danielson 1991), or, to include the effect of human influence, *an aggregate of different but interacting elements, sometimes united by a cultural attribute* (e.g., an agricultural landscape of cultivated fields, pastures, stockponds, and hedgerows) (Bolen and Robinson 1995). These well-framed definitions are important because the fundamental goal of conservation biology – the preservation of biodiversity – rests largely upon the conservation, preservation, and management of habitat and landscape. Habitat distribution is a primary determinant of species' abundance, and it is often the degree of habitat specificity that determines whether a species is common or rare (Rabinowitz et al. 1986). Habitat and landscape considerations are fundamental to all forms of ***geographic-based approaches*** to biodiversity conservation. As opposed to population-based approaches, a geographic-based approach focuses less on the individual dynamics of a particular population and more on the qualities of habitat and landscape that sustain it and other populations. The role of habitat and landscape are vital to population persistence, especially because populations become more susceptible to extinction in the face of environmental variation. For example, prolonged drought can pose a threat to wetland-dependent species because some wetland habitats disappear. Environmental variation cannot be eliminated even in large reserves, but the preservation of habitat, for example, wetland preservation, at landscape, regional, or global scales, can reduce adverse effects of such variation and conserve essential, habitat-specific resources needed by every species.

Today many conservation biologists consider habitat alteration the single greatest threat to species and ecosystems worldwide (Soulé 1991; Noss and Cooperrider 1994). Habitat alteration includes the physical conversion of natural habitat to an unnatural habitat (habitat loss), the breaking of large, contiguous blocks of habitat into smaller patches (habitat fragmentation), the increasing separation of blocks of habitat from one another (habitat isolation), and the changes in a habitat that affect its composition, structure, or function (habitat degradation) (Noss et al. 1997). But why do habitats matter so much in the conservation of individual species?

10.1.2. How Do We Measure Habitat Use?

10.1.2.1. An Example in Moose: Habitat Choices of a Habitat Generalist

Faced with an array of habitats in a particular landscape, a mobile species, such as a moose (*Alces alces*) can choose which habitats to use. Figure 10.1 gives a summary of these choices, using a sample of radio-collared moose from a larger population (Van Dyke et al. 1995). Habitat classification like this requires the creation of arbitrary categories, but by creating such categories we can analyze the distribution of animals in a matrix of complex vegetation. These data and their interpretation offer some insights into principles of how animals use habitat, and why understanding species-specific habitat relationships is important to conservation.

Note that moose, like most species, use more than one kind of habitat. This is because a single habitat seldom provides all necessary resources for a species to accomplish various essential activities over its life span, including

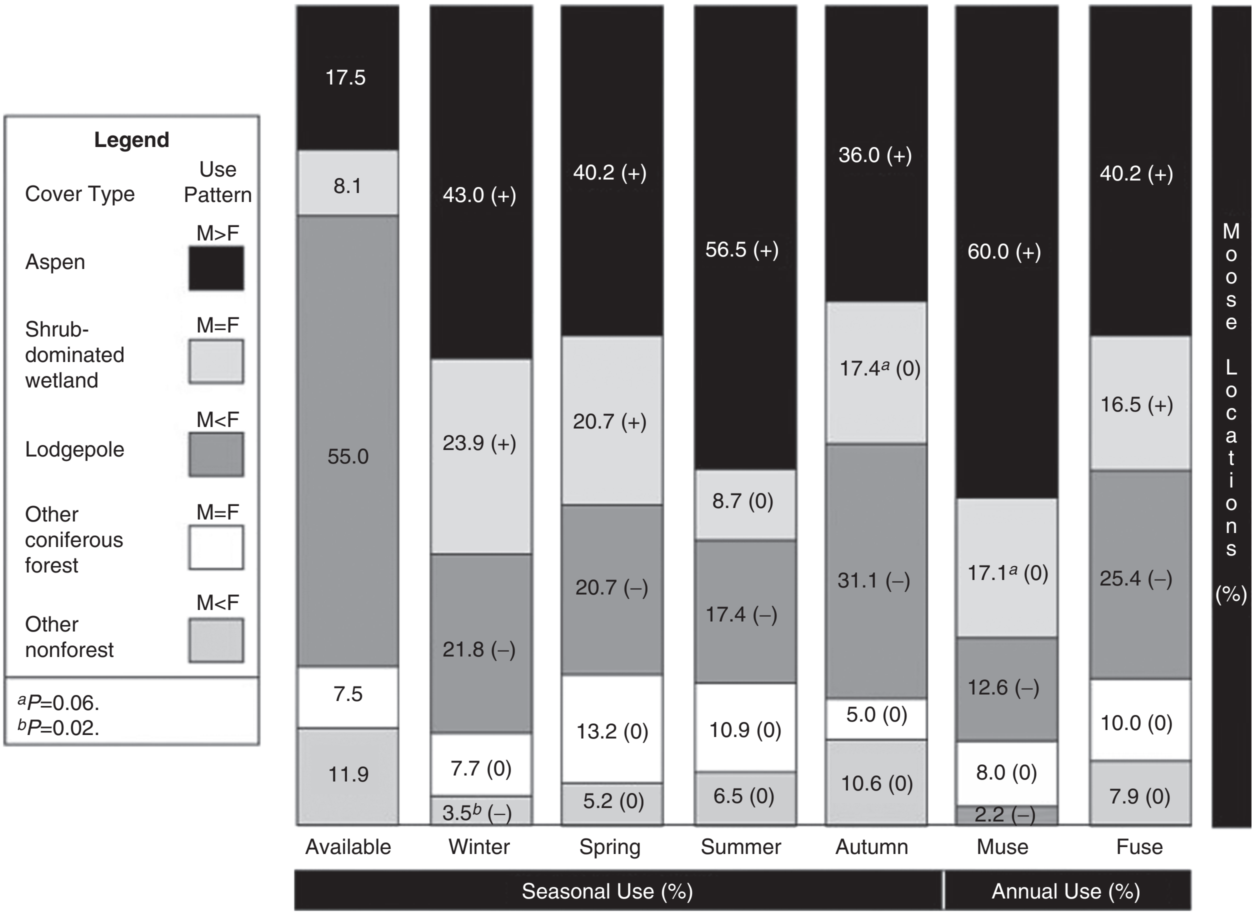

FIGURE 10.1. Seasonal habitat selection by three male and ten female moose in the Fiddler and Fishtail Creek drainages, south-central Montana, USA, 1989–1993. Numbers indicate percentages. Symbols in parentheses indicate selection for (+), selection against (–), or no selection (0). $P < 0.01$ (simultaneous confidence intervals, Marcum and Loftsgaarden 1980) for all cases of selection and for differences between sexes, except where noted. (Based on data from Van Dyke et al. 1995. Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

survival and reproduction. Second, habitat *use* is often different from habitat *availability*. Some habitats are used at rates greater than expected, whereas other habitats are used less often than expected relative to their distribution in a landscape. These differences provide clues that can lead conservationists to make well-informed hypotheses about why patterns of apparent habitat preference or avoidance appear in particular species. If these hypotheses are tested through careful experimental design and manipulation, the results of the experiments can provide insight about reasons animals choose habitats, and about the resources that habitats provide to the animals. Third, these data also demonstrate the principle that habitat use changes over time (in this case, seasonally). Such changes should be expected because the availability of resources in habitats changes temporally and seasonally. Although obvious, this fact has often been overlooked in the design of parks and nature reserves. If the full array of habitat and landscape structure that animals require in different seasons does not exist within the reserve, then they must leave the reserve to find it or perish in the reserve without it. Habitats, like organisms, have "life spans," so provision must be made to create new habitat as well as to preserve existing habitat. Fourth, habitat use differs among individuals. Sex- or age-related differences in body size, social organization, or investment in reproductive effort and parental care lead individuals of the same population to select different habitats during the same period of time. Failure to consider these differences can lead to inappropriate choices of which habitats to conserve and result in ineffective conservation efforts.

Looking beyond these insights, there are other reasons why habitat is important to conservation. (1) Arrangements of habitat patches and distances between patches of the same type of habitat, along with the presence or absence of connecting habitat corridors, may influence individual movement and population persistence. (2) Movement of conspecifics among habitat patches can affect population dynamics, social behavior, rates of extinction, and genetic composition of populations. (3) Different species respond differently to a given array of habitats. (4) Movements of other species in and out of and among habitat patches may be important to a species of conservation interest. (5) Spatial configurations of patches can affect processes of populations and communities (Lidicker 1995). The first problem to be solved is: how do we determine which habitats are important to species of conservation interest?

10.1.2.2. Measuring Habitat Selection and Preference

There are many algorithms that can use these kinds of data for making assessments of such differential use of habitats by individuals and populations. One such algorithm for identifying the strength of selection for habitats is Ivlev's Selection Index (Ivlev 1961). Originally developed to assess selection for food items, it can be effectively applied to measure selection for habitat as well (Yeo and Peek 1992). Ivlev's index of selection (*SI*) for a given type of habitat is determined as

$$SI = (U - A)/U + A$$

where U is equal to the proportion the animal's use of the habitat out of all use and A is the proportion of the same habitat available in the landscape. For example, suppose it can be determined that an animal spends 80% of all its time in stands of aspen (*Populus tremuloides*) trees ($U = 80$) within a home range in which aspen stands make up only 10% of the landscape ($A = 10$). In this case

$$SI = (80 - 10)/(80 + 10) = 70/90 = 0.78.$$

Note that, in Ivlev's formula, the selection index will be zero whenever the animal uses the habitat in the same proportion as its availability (no selection). It will approach the value of 1 when use is proportionately much higher than availability, as in our example, suggesting strong preference for that habitat. Alternatively, it will approach a value of negative one when use is far less than availability, suggesting avoidance of the habitat. If many samples of habitat use are made from multiple individuals in the same area, standard statistical techniques can be used to see if the average value of the selection index is different from zero (Neu et al. 1974; Marcum and Loftsgaarden 1980).

To acquire data on the availability of habitat in an area one can use existing vegetation maps, aerial photos, or files of geographic information systems. If none of these exist, availability can be determined from sampling numerous random points within the area until an appropriate number of samples have been made. Use of habitats by an animal can be determined from direct observation, from radio telemetry data, from systematic trapping, or from determining the locations of songs, tracks, or sign (scat or markings). Regardless of method, there will always be some feasible way of obtaining some estimate of habitat use relative to availability, and then using such information to make a more informed decision about which habitats to preserve for particular species. Of course, knowing the habitat needs of individual species is not enough. One of the most serious challenges facing conservation managers today is to understand how to manage habitat for multiple species groups and their associated interactions. A first step to progress in solving these and other problems is to begin to understand basic characteristics and properties of habitats. These include the concepts of habitat heterogeneity, landscape gradients, and patch dynamics.

10.2. Heterogeneity, Landscape Gradients and Patch Dynamics

10.2.1. Habitat Heterogeneity, Gradients, and Patchiness

It is not sufficient to know what habitats a species might prefer to use. We must also know how habitats are distributed. A persistent characteristic of habitats is that they are highly variable in space and time, a quality referred to as ***habitat heterogeneity***. Habitat heterogeneity can be defined as *any form of variation in the environment, including physical and biotic components. Such variation may appear as spatial or temporal patterns* (Ostfeld et al. 1997). Broadly, there are primarily two types of models that explain habitat patterns in landscapes. ***Patch models*** assume that heterogeneity exists because habitats occur in *patches*, which can be defined as *an area, smaller than a landscape, that contains only one type of habitat* (Danielson 1991). ***Patchiness***, a description of habitat arrangement, can be defined as *a form of spatial heterogeneity in which boundaries may be discerned. Patchy heterogeneity appears as contrasting discrete states of physical or biotic phenomena*. (Ostfeld et al. 1997). This "patch model" of landscape heterogeneity is appropriate to describe the spatial structure of some ecological systems, especially those in which there are clearly defined boundaries or edges between different kinds of habitat, and is often accurate and applicable at larger landscape scales. In landscapes with habitat arrangements that fit the patch model, species richness and species diversity will be correlates of habitat heterogeneity and patchiness.

In many systems, however, a ***gradient model***, in which boundaries between different habitats are not clearly defined and environmental conditions (variables) change slowly and gradually at fine spatial scales, provides a more accurate description of ecological reality. Gradient models are often most applicable in environments where the distribution of organisms, particularly plants, is strongly affected by one or more continuously varying environmental variables, such as moisture, elevation, temperature, or the concentration of a particular soil nutrient or soil type. When this is the case, habitat "patches" may not be easily discernible, and the distribution of organisms, as well as community biodiversity, is better modeled and more easily explained by tracking and predicting changes in the controlling variables. Gradient models can be especially predictive at smaller, microhabitat scales, but in some ecosystems they are also applicable at much larger scales, such as in Oregon forests, in which the distribution of vegetation and assocaiated habitat is strongly influenced gradients in temperature and moisture (Ohmann and Spies 1998).

The realities of heterogeneity, patchiness, and gradients can cover a wide spectrum of conditions. At one extreme, patches of habitat can be entirely discrete and perfectly discernible from one another. At the opposite extreme, the habitat, although heterogeneous, may have subtle and almost imperceptible gradations from one kind of patch to another. A patchy landscape often has a rich internal structure of different habitats, although sometimes with only gradual differences in environmental conditions across spatial scales. In any form or at any scale, patchiness and gradients create a discontinuity of resource distribution that provides a variety of niches and species to exploit them. Thus, heterogeneity, patchiness, and environmental gradients are dominant influences in habitat composition and landscape structure, and their biodiversity.

10.2.2. Habitats and Landscapes: Understanding Scales of Space and Time

Habitats, whether consisting of discrete patches or of gradient-associated habitats with indiscernible boundaries, are ultimately heterogeneous. Perceiving their heterogeneity depends on the spatial and temporal scales used to measure it. Habitat and landscape structure are not constant but change over time and space. The higher the rate of landscape change, the lower the probability of regional population survival (Fahrig and Merriam 1995). Environmental heterogeneity associated with and, to an extent, determined by the landscape is a function of spatial and temporal heterogeneity. In turn, spatial and temporal heterogeneity are functions of the intensity and frequency of landscape disturbance. Each must be considered to understand how to conserve and manage habitat. Therefore, the analysis of habitats and landscapes, and the efforts to conserve them, must treat scale as an explicitly stated variable when we attempt to understand and conserve habitat and landscape.

Habitats may be classified at multiple scales of heterogeneity, but organisms respond to habitats at particular scales. Begin with a scale of time. To a casual observer, habitats give an impression of being permanent landscape features, but they are not. Just as we speak of "population dynamics," it is just as appropriate to speak of "habitat dynamics." Temporal scale can be defined as *habitat lifespan relative to the generation time of the organism* (Fahrig 1992). If the life span of the habitat is short relative to that of the organism, organisms must enter periods of dormancy to endure non-habitat environments until the habitat reappears, or employ nomadic behavior or high rates and distances of dispersal to reach other suitable habitat. If the life span of the habitat is long relative to the organism, sedentary behavior and more limited dispersal are favored.

To appreciate and analyze effects of spatial and temporal scale independently and synergistically, Lenore Fahrig created a stochastic model of habitat-organism interactions that evaluated the relative importance of each on population persistence. Imagine a two-dimensional model universe of habitat "cells" of two categories, "useable" habitat cells in which organisms can survive and reproduce, and "non-useable" habitat cells that are inhospitable. The usable cells are clustered as "habitat patches." They are not only clustered but transient, existing only for a limited time. New habitat patches appear at random at discrete time intervals ("steps"). Fahrig's model is simple, containing only six constants (fraction of grid in useable habitat, per capita birth rate per time step, death rate per time step, age of organism at maturity, maximum population per habitat cell, and fraction of population dispersing per time step) and three variables (lifespan of patches L, size of patches S, and mean dispersal distance Z) (Fahrig 1992). In each time step, four events occur in sequence: (1) habitat patches are "born," (2) some organisms survive and reproduce while others die, (3) some survivors disperse to new patches, and (4) some patches "die."

By holding the amount of habitat constant but varying values of patch lifespan, patch size and species dispersal distance in different combinations, Fahrig was able to independently evaluate the effects of temporal and spatial scale on population size. The model's outcomes showed that populations increased with increasing ***temporal scale*** (i.e., densities of organisms increased the longer a given patch of habitat persisted) and decreased with increasing ***spatial scale*** (i.e., as the ratio of distances between patches to the organism's average dispersal distance increased, densities of organisms declined). In relative importance, temporal scale had a far greater effect on population stability than spatial scale (Fahrig 1992). At any spatial scale, populations were larger when habitat patches persisted longer (Figure 10.2).

Important insights emerge from this model. If the goal of a conservation effort is to preserve a particular species, conservationists must determine the temporal scale of its preferred habitat. Is its favorite habitat persistent relative to the life of the organism (high temporal scale), or are preferred habitats ephemeral, appearing unpredictably and disappearing frequently? Because temporal scale may be more important than spatial scale, size of reserve fragments may be less important than their persistence. Fahrig goes on to recommend that "since habitat continually

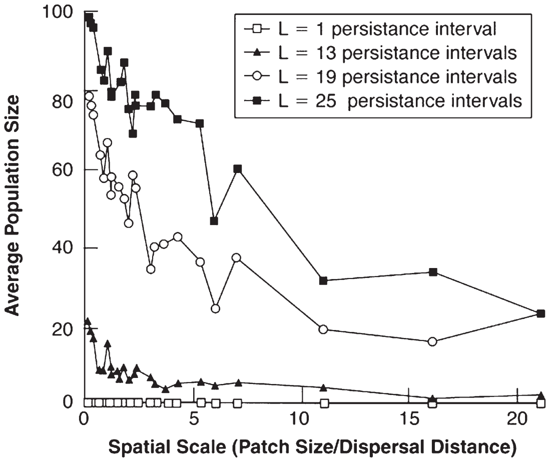

FIGURE 10.2. The effect of spatial scale on mean population size at four different levels of habitat persistence. Note that as habitat persistence (temporal scale) increases, average population size rises. (Fahrig 1992. Copyright 1992. With permission from Elsevier.)

undergoes modification due to processes such as disturbance … more attention should be placed on the duration of reserve fragments as habitat for particular species of interest" (Fahrig 1992). Good advice. The question is, can we predict changes in habitat along a temporal scale?

10.2.3. How Do We Predict Habitat Change?

10.2.3.1. Predicting Habitat Transitions Using a Markov Model

We have already examined how to build models that evaluate the viability of individual populations through time (population viability analysis models, Chapter 8). Can we also construct useful models that tell us something about how landscape structure might change over time? The answer is yes, and in much the same way. Let us begin with a simple, but nevertheless useful, approach that requires us to follow five steps in explicating the characteristics of a landscape. For our database, we will need to know what habitats or cover types are present today and their locations, and we will need to know what habitat or cover types were present in the same places at some time in the past. Let us represent the number of cover types by the symbol m. We might get information on cover types from maps, photographs, satellite images, vegetation surveys, or files from Geographic Information Systems (GIS). For the record, let us call the past point of our records time t, and our present point in time $t + 1$. Now, for the steps. First, divide landscape into cells and identify the habitat or cover type in each one of them. Second, tally all the cells in which cover type in the cell changes from time t to time $t + 1$. Third, summarize all the tallies of all m cover types in an $m \times m$ matrix. Fourth, note that an individual element of the matrix, n_{ij}, (the number in the cell specificed by the intersection of row i and column j), represents the number of cells that changed from cover type i to cover type j over the studied time interval. In the fifth step, divide each matrix element, such as n_{ij}, by its row total to generate the transition matrix P in which a given matrix element, such as p_{ij} of P summarizes the *proportion* of cells that changed from cover type i to cover type j during the studied time interval. For example, suppose that in the matrix at time t, the total number (tally) of cells classified as "aspen" is 20. Now suppose that, at time $t + 1$, on 14 of the 20 cells "aspen" has been replaced by "lodgepole," 2 cells remain "aspen," 2 are replaced by "spruce" and 2 by "meadow." The row total is therefore $2 + 14 + 2 + 2 = 20$, and the probability that aspen will be replaced by lodgepole is 14/20 or 0.7 (Table 10.1). The diagonal elements in the matrix, p_{ii}, represent the proportion of cells of each cover type that did not change (***stasis rates***). We can repeat this procedure for every habitat or cover type, and thus determine a transition rate for every habitat transition that occurs over the time interval (Urban and Wallin 2002).

Notice the similarity of this transition matrix, and the procedure to create it, to that of a transition matrix for a stage-based population model (Chapter 8). They are similar because both use the same structure, the Markov model. A Markov model assumes that to predict the state of the system at time $t + 1$ one need only know the state of the system at time t (Usher 1992). The heart of a Markov model is the transition matrix P, which summarizes the probability that a cell in cover type i will change to cover type j during a single time step, whether we are talking about habitats or organisms. The time step is the interval over which the data were observed to change. Markov models, although simple, can be solved by iteration to project the state of the system in the future.

The predictions of habitat change generated by the Markov model are important considerations in determining an optimal conservation strategy because extinctions of individual populations are common in habitat patches. Recolonization of populations following extinction depends upon the distances between occupied and unoccupied patches (landscape spatial structure), the rates and distances of dispersal by the organism (dispersal characteristics), and the length of time that habitat patches persist (temporal changes). The stability of the community will depend on whether a species is likely to replace itself after a disturbance or whether it is likely to be replaced by another species. If changes in landscape structure occur at an unnaturally high rate (as in some anthropogenic changes), neither dispersal nor adaptation can keep up, and the result is a high rate of local and regional extinction.

TABLE 10.1. The transition matrix of a Markov model that permits prediction of transitions in habitat states from time t to time t+1. In this matrix, the total number (tally) of cells classified as "aspen" is 20. In 14 of the 20 cells "aspen" has been replaced by "lodgepole" and 6 remain "aspen". The row total of aspen is 2 + 14 + 2 + 0 + 2 = 20. The value of an individual transition rate, p_{ij}, such as that from aspen to lodgepole ($p_{aspen\ to\ lodgepole}$), is equal to 14/20 or 0.7, the probability that aspen will be replaced by lodgepole over the observed time span. The diagonal elements in the matrix represent the number of cells of each cover type that did not change (stasis rates).

t ╲ t + 1	Aspen	Lodgepole	Spruce	Douglas fir	Meadow	Total
Aspen	2	14	2	0	2	20
Lodgepole	4	14	0	1	1	20
Spruce	2	10	7	0	1	20
Douglas Fir	1	4	1	13	1	20
Meadow	5	3	6	3	3	20
Total	14	45	16	17	8	100

The interaction between the rate of change in landscape spatial structure and the rate of change in dispersal behavior determines the probability of a species' regional survival. As long as the rate of change in dispersal behavior is greater than the rate of change in landscape spatial structure, it is possible for the organism to survive in the changing landscape by moving around in it and integrating its resources over space. For example, in unaltered habitats of woods or brush in the eastern US, the white-footed mouse uses home ranges of less than 0.5 ha. When agricultural clearing fragments woodland habitat, home ranges increase to tens of ha and mice may move hundreds of meters in one night (Merriam and Lanoue 1990; Wegner and Merriam 1990). Similarly, the red fox (*Vulpes vulpes*) disperses farther in fragmented urban habitats than in less fragmented boreal forests (Lindstrom 1989; Hansson 1991). Although organisms like mice and foxes can adapt their dispersal distances to changes in landscape structure, each species has a maximum possible rate of change in dispersal behavior. If landscape structure is changing faster than this, the organism will be unable to recolonize areas where local extinctions have occurred at a sufficient rate and the regional population will become extinct (Fahrig and Merriam 1995).

Both traditional and contemporary efforts in conservation have focused on issues of spatial scale (i.e., preserving local populations in local places). But such efforts, without considerations of temporal scale, may not conserve habitats or populations. Because rates of change in habitat and landscape structure have larger effects on populations than arrangements and distances between habitats, preserving habits and species alone is not a sufficient condition for long-term population and habitat persistence. Only conservation efforts that incorporate temporal, as well as spatial, management of landscape processes will be effective in the long run. This means that conservation biologists must be able to manage patterns of habitat change through time. That is, they must be able to manage patterns of ***ecological succession***.

10.2.3.2. Habitat Transition in Conservation – Managing the Successional Process

Changes in habitat predicted in the Markov model are often expressions of ecological succession, a pattern of continuous, directional, and non-seasonal change (replacement) of plant populations on a site over time. A shortcoming of Markov models is that they are deterministic rather than stochastic, and therefore assume that the past is a reliable predictor of the future. Aside from the generic problems inherent in deterministic models which we have explored previously in the context of modeling populations (Chapter 8), an additional problem for Markov models is that their assumption of making the past a predictor of the future may not be true under current dynamics of global climate change (Chapter 5). Therefore, more sophisticated process-oriented stochastic models simulating landscape dynamics, such as the LANDIS model, which has been used to predict change in forest landscapes over time, may be more appropriate and realistic for predicting succession. LANDIS, for example, is a spatially explicit landscape simulation model that uses inputs on fire frequency, size, and intensity, species-specific fire resilience, windthrow, and harvest disturbance (logging) to make predictions of species level succession (He and Mladenoff 1999), and is capable of stochastically incorporating variables such as temperature, precipitation, and land use (Gustafson et al. 2003; Sturtevant et al. 2004). Thus, process-oriented stochastic models like LANDIS provide an alternative approach that can be more reliable in their predicted outcomes under conditions of dynamic landscape and climate change.

Regardless of the types of modeling tools that managers might use to predict habitat change in landscapes, managing such change over time is an exercise in managing succession. Succession in a habitat can be managed toward the goals of conservation in three ways. First managers can alter the frequency, extent, and intensity of disturbance events by applying fire, flooding, cutting, herbicides, or mechanical methods of vegetation removal at varying intervals. The second way is to manage succession by altering plant and animal interactions. One means to this end is to manipulate the density of herbivores on the site following disturbance. Manipulations can range from no control, which often leads to heavy use of vegetation by herbivores and significant impacts on the amount and composition of vegetation, to total exclusion of herbivores, a strategy that often produces communities of high plant biomass but low net productivity. A third way is to change the availability of species that can invade a disturbed site. For example, range managers restoring a degraded prairie might first burn the site and then seed it with native species that represent the system that will function best on that site, or that are of particular value for conservation. In a forest, sites disturbed by logging may be arranged close to abundant seed sources of desired species, or such species may be planted directly on the site when logging is completed. Similarly, wetlands created by deliberate flooding may be seeded with species of value to conservation or that have value as food and cover for wetland wildlife. The same approach can be employed, in a negative way, through species-specific herbicide application after the disturbance event, thus altering the pattern of succession. A fourth way of managing succession is to manipulate the availability of resources at a site, and so alter the interactions of plants with the environment and with other species. Adding specific nutrients and fertilizers to logged sites in forests or to cleared or burned areas in prairies to favor the establishment of particular species is a common management practice. Removing undesirable species from sites after disturbance may be done to favor species considered more beneficial to system function, more valuable for animals, or of greater value in conservation. Leaving resources in place, such as snags, following a logging operation, can increase the availability of nest sites for cavity-nesting birds.

Can a conservation biologist employ multiple methods of managing succession simultaneously to attain a conservation objective? Yes, but to do so requires ingenuity. One example of an initiative that used multiple approaches in succession management is Johnson and Leopold's (1998) effort to manage habitat for the endangered eastern massasauga rattlesnake (*Sistrurus catenatus catenatus*). The massasauga uses non-forested wetlands throughout its range in the eastern United States and Canada, preferring early successional communities. It suffers habitat loss as succession proceeds, especially from encroachment of woody plants into wet meadows.

Johnson and Leopold applied the first approach, directly altering the type, frequency, and intensity of disturbance events, by cutting and burning all woody vegetation in selected experimental plots in the Cicero Swamp Wildlife Management Area in New York (USA), a peatland complex inhabited by massasaugas. They then made use of the second approach, altering plant and animal interactions, by enclosing selected plots in wire fences, thus excluding herbivores (primarily white-tailed deer). Finally, by applying herbicides specific for woody vegetation combined with cutting, Johnson and Leopold employed the third approach, and altered the pattern of plant invasion subsequent to the disturbance.

Over 3 years, Johnson and Leopold were successful, to varying degrees, in altering patterns of succession through these approaches, particularly in achieving reductions in the density, basal area, and height of shrubs in treated plots compared to untreated areas, and, with herbicides, increasing the rate of mortality and decreasing the rate of resprouting among woody species. Although the response of the massasauga to the treatments was inconclusive and limited by a small sample size (nine radio-marked massasaugas), massasaugas did use treated areas at more than four times their availability (10.1% of locations in treated areas that made up only 2.5% of the total area).

Johnson and Leopold's effort illustrates the role and value of managing succession in conservation. That should not surprise us. In general, ecological models based on habitat succession have proven more accurate at predicting the distribution of organisms than null models (models based on random environmental fluctuation) or isolation models (models based on island biogeography theory and metapopulation theory) (Kareiva et al. 1997). Both habitat conservation and species conservation, which are intimately related, require management of succession.

POINTS OF ENGAGEMENT – QUESTION 1

How would the perspectives and activities of a reserve manager change if he or she changed the goal from achieving a *state* (e.g., a proportional abundance of a desired habitat or a targeted population level of a particular species) to enhancing a *process* like ecological succession? What specific changes can you imagine in allocations of time, questions of research interest, and desired outcomes if such a change occurred?

10.3. Problems of Habitat Loss, Isolation, and Fragmentation

10.3.1. Neutral Landscape Models and the Isolation of Effects

Intuitively, we perceive that habitat fragmentation is a process that will be detrimental to most species. But why is this so? To understand the problem of habitat fragmentation and the basis of its detrimental effects, we must begin with an appropriate theoretical framework for landscape-scale ecological and population processes and the effects of fragmentation on them. To achieve this, we must start by separating and clarifying three related but distinct processes that degrade or destroy habitats. These are ***habitat loss***, ***habitat fragmentation*** and ***habitat isolation***. Then, as these processes occur, we must understand and clarify the effects of ***edge influences*** (EI) that begin to increase in strength in fragmented habitats and lead to habitat degradation.

We often observe that the process and effects of habitat destruction and degradation follow a predictable sequence. (1) A block of contiguous habitat is reduced in size by conversion to non-habitat (habitat loss) and increasingly broken into numerous smaller patches (habitat fragmentation). (2) Remaining patches decrease in size and number because of increased vulnerability to disturbance and invasion by other species and increased ease of alteration or removal by humans. (3) Distance between patches increases (habitat isolation). (4) Quality of the patches decreases (degradation) as (5) the importance of EI increases (Oksanen and Schneider 1995). Although loss, fragmentation, isolation and degradation can occur concurrently, they must first be analyzed separately to be clearly understood.

One approach to modeling the problem of habitat loss, fragmentation, isolation, and degradation is through a class of models known as ***neutral landscape models***, in that distribution of habitats in the landscape is a theoretical distribution of habitat independent of (i.e., "neutral" toward) actual biophysical processes that shape landscapes. Neutral landscape models are attractive because they can serve as "null" models or statistical baselines for exploring the effects of spatial patterns of habitats in landscapes on population persistence and growth, and because they can be created simply.

In neutral landscape models, the landscape is represented as a grid (*lattice*) of area m^2 in which some fraction (p) of the grid cells (sites) are "filled" or "occupied" with a type of habitat in which an organism can live and reproduce. In contrast, "empty" or "matrix"cells of non-habitat are arranged among the "filled" habitat cells. How would an organism relate to this model landscape? The "connectedness" between the model's habitats, or, ***habitat connectivity*** of the model, is determined by the model's ***neighborhood*** or ***movement rules***, which specify the distance across which sites are accessible to organisms by virtue of their dispersal or gap-crossing abilities. Thus, the critical threshold of habitat abundance (p_c) at which the habitat connectedness is lost and the landscape becomes "disconnected" shifts to increasingly lower levels of habitat abundance (p) as the movement neighborhood becomes larger; that is $p_c \rightarrow 0$ as the "neighborhood size" (the area that organisms can disperse to) approaches m^2 (the size of the landscape). Therefore, organisms with good dispersal abilities should perceive landscapes as connected across a greater range of habitat abundance (and levels of fragmentation) than do those constrained to move only through habitat cells. By creating movement rules using dispersive abilities of individual species and their tolerance to non-habitat (matrix) conditions, conservation biologists can create models based on actual species' perceptions of landscape structure. They can then begin to look at landscape connectivity from the perspective of an individual species, and this approach permits the development of more effective conservation strategies. As landscape ecologist Kimberly With puts it, "Determining the scale at which organisms are able to interact with the landscape pattern is thus the key to defining landscape connectivity" (With 2002a:109).

10.3.2. Percolation Theory: Defining the Critical Threshold of Fragmentation

> *How many red spots make a white cow red?*
> *How many clearings make a forest, prairie?*
> *A score? More? A coalescing core?*
> *A threshold reached?*
>
> (Forman and Godron 1986)

Scientific textbooks are not normally known for good poetry, yet this cryptic but subltly disturbing verse from Forman and Godron's classic text, *Landscape Ecology*, captures the essence of a critical conservation question. At what point in the process of habitat and landscape fragmentation is a critical threshold reached, beyond which a formerly contiguous unit of habitat and its resident species will rapidly degrade and decline? And can be predict where this point will occur, and prevent it?

Over 20 years ago, Jerry Franklin of the US Forest Service and the aforementioned Richard Forman of Harvard University offered a detailed analysis of the ecological consequences of historic patterns of timber harvest in US Pacific Northwest forests in the first issue of the (then) new journal, *Landscape Ecology*. In their groundbreaking paper, "Creating landscape patterns by forest cutting: ecological consequences and principles," Franklin and Forman examined the projected long-term effects of the then current management practice of "staggered-setting clearcutting," in which 10–20 ha patches of clearcuts were interspersed with uncut forest areas of at least equal size (Franklin and Forman 1987). These scientists noted prophetically that "…the ecological and economic appropriateness of this system should be reexamined … evidence is accumulating that this system … increases the risk of some types of catastrophic disturbance" (Franklin and Forman 1987:6). Specifically, Franklin and Forman determined that "at about the 30% cutover point, the average [uncut] forest patch size begins to drop sharply … because cuts coalesce into continuous lines of patches dividing the previously continuous forests into sections" (Franklin and Forman 1987:8). Why does this happen? When less than 30% of the forest

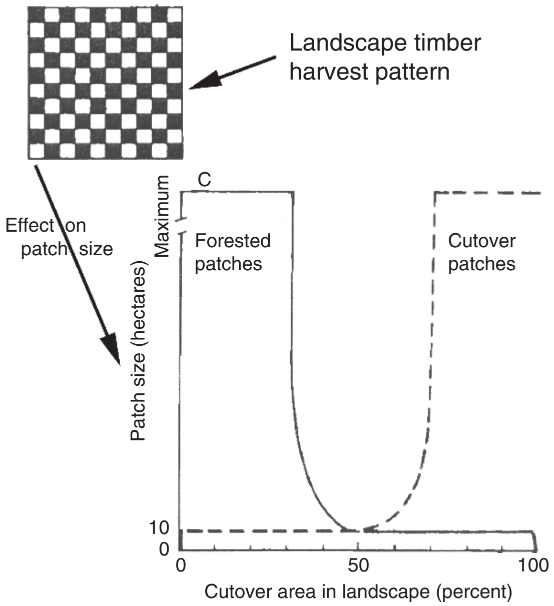

FIGURE 10.3. Changes in landscape characteristics along a timber cutting gradient based on regularly distributed dispersed (checkerboard) patch cuttings (clearcuts) of 10–20 ha. Note the precipitous decline in the average patch size of uncut forests when the landscape reaches the 30% cutover point (clearcuts cover 30% of the forest). (Franklin and Forman 1987. Copyright 1987 Springer-Verlag, New York, Inc. With the kind permission of Springer Science and Business Media.)

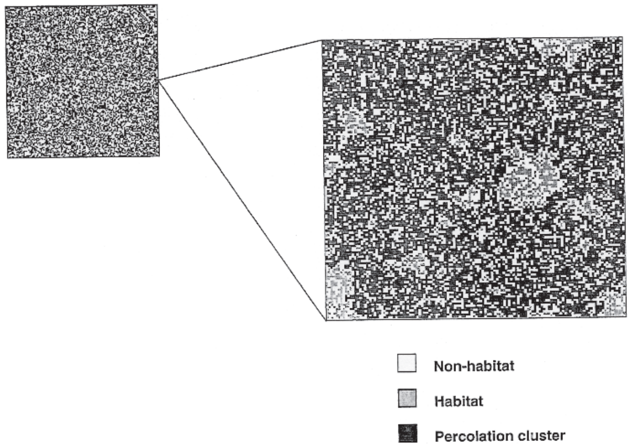

FIGURE 10.4. The percolation cluster of a random, computer-generated landscape where p_c, the critical fragmentation threshold, is 0.6. As long as 60% of the landscape remains "habitat," all parts of the habitat in the landscape are "connected," and in sufficient proximity to permit movement of organisms from one portion to any other. (With 2002. Copyright 2002 Springer-Verlag, New York, Inc. With the kind permission of Springer Science and Business Media.)

has been cut, the cuts that have been made are still relatively small gaps in an extensive and relatively continguous forested landscape. But when this critcal cutover point is reached, the landscape loses it contiguous character (Figure 10.3). How can we understand this case history from a theoretical basis, and what are the implications for conservation?

If the dispersive abilities of the organisms remain large relative to the separation distances between habitats created by the matrix cells, the system remains "connected." For example, in a model depicting an undisturbed area, a single group of connected habitat patches, or "cluster," might span the entire system (i.e., there would be connectedness or "flow" between all habitat cells). Here there is overall connectivity because flows can *percolate* across the entire system, and the spanning cluster is therefore called the ***percolation cluster*** (Figure 10.4) (With 2002b). ***Percolation theory*** is the quantitative analysis of connectivity in spatially structured landscape systems. In its original context, percolation theory was first developed in the 1940s by physicists to describe the physical properties of gels, polymers, and glassy materials, particularly as a means to understand the flow of liquids through material aggregates. In the 1980s, at the same time that Franklin and Forman were describing the results of their analysis of forest clearcuts, landscape ecologists Robert Gardner and Robert O'Neill of Tennessee's (USA) Oak Ridge National Laboratory and their colleagues saw the potential applications of percolation theory to the problems of landscape ecology and habitat fragmentation, and began to incorporate it into neutral models for describing landscape patterns (Gardner et al. 1987). At a landscape level, percolation theory can be understood in this way. Stochastic disturbances that disrupt linkages among sites (e.g., disturbances that destroy habitat sites) reduce the size of the percolation cluster until it fragments and the system no longer percolates (flows cannot occur between habitat cells). The level of disturbance (e.g., the proportion of sites destroyed) at which the transition from a connected to a disconnected system occurs is called the ***critical*** or ***percolation threshold,*** denoted earlier as p_c. The percolation threshold is defined as the level of habitat abundance (p) at which the probability of having a connected landscape (defined by percolation frequency) is less than or equal to 0.5. Above this value, the landscape is considered to be connected; below the threshold, the landscape is disconnected (With 2002b:214). Thus, a percolation cluster is really a definition of a kind of step-function or threshold such that the probability of the landscape containing a spanning cluster goes from near 1 (certainty) to near 0 (non-existent) over a very small range of p. Above the threshold ($p > p_c$), the probability of having a percolation cluster is high and the largest cluster is the percolation cluster, which dominates the system. Below the threshold ($p < p_{(c)}$), no percolation cluster occurs and the system consists of numerous small clusters (i.e. the system is disconnected). Thus, above this threshold, habitat destruction results in *loss of habitat* but not in loss of *connectedness of habitat*.

10.3.3. Can Percolation Theory Explain the Real World? Models and Field Studies

10.3.3.1. Habitat-Population Models Support the Predictions of Percolation Theory

Percolation theory predicts that transition from a connected to an unconnected habitat will be abrupt, thus the effects of fragmentation will appear suddenly when the *amount* of habitat in a landscape reaches some critical value. Is there evidence that this would really happen? To start with, what do other landscape models predict?

US Forest Service Research Scientists Curtis Flather, Michael Bevers, and John Hof developed a model designed to evaluate the effects of fragmentation on a hypothetical "species" of bird. Their landscape was composed of cells arranged in a 32 × 32 matrix (1,024 cells) in which each cell was assigned a category of habitat or non-habitat. Flather and his colleagues allowed the actual amount of habitat in the landscape matrix to vary from 10% to 90%, changing in 10% increments, creating nine different levels of habitat variability. They also specified one of nine different levels of fragmentation of the landscape, from highly fragmented to highly aggregated, thus producing 81 different combinations (9 × 9) of availability and fragmentation. Into this landscape they introduced a generic, computer-generated "bird species," that bred in habitat cells, defended a territory equal to the area of one cell and, therefore, had a carrying capacity of one breeding pair per cell (Flather et al. 2002). With these specifications, Flather et al. also defined movement rules that permitted the birds' offspring to move to new habitat cells, but the probability of reaching a new cell declined with distance from the natal cell.

In this model, as long as the amount of habitat was greater than 40%, it was the *amount* of habitat that had the greatest effect on population size, accounting for 97% of the variation in abundance (Figure 10.5a, Table 10.2) and the probability of the population's persistence was near 1.0 (Figure 10.5b). Fragmentation levels, which affected *arrangement* of habitat, was inconsequential. However, if the amount of habitat dropped to 40% or lower, the probability of the population's persistence in the landscape dropped suddenly (Figure 10.5b) and the degree of fragmentation of remaining habitat became a major factor in

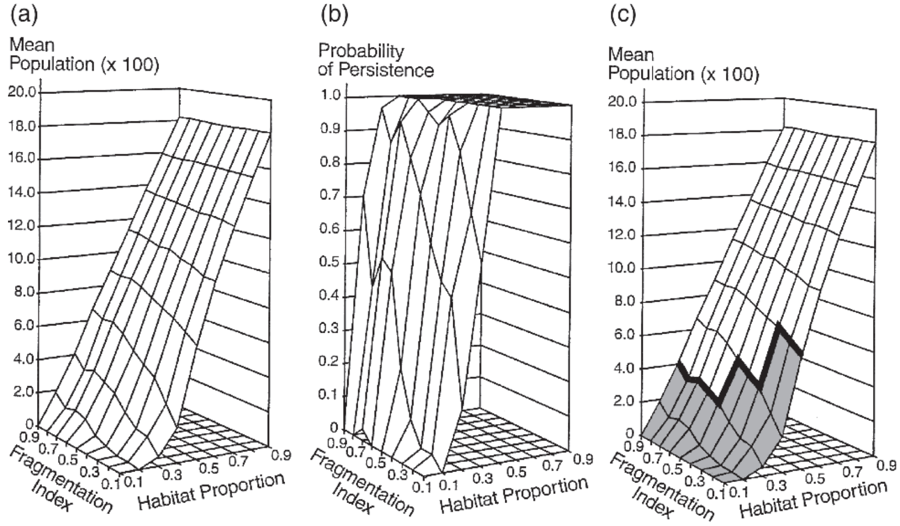

FIGURE 10.5. Population response of a hypothetical species to simulated landscapes with specified amounts of habitat and levels of fragmentation. As long as 50% or more of the landscape remains in suitable habitat, variation in the amount of habitat accounts for 97% of the variation in population size (a) (See Table 10.2). When the amount of habitat in the landscape drops below 50%, the probability of the population's persistence declines rapidly. (b) Below this level of habitat, degree of fragmentation now becomes an important factor in population persistence, with the *persistence threshold* (c, shaded) of the population dropping sharply and suddenly at critical levels of fragmentation ("stairstep" regions) in a landscape with reduced habitat. (Flather et al. 2002 Copyright 2002 Springer-Verlag, New York, Inc. With the kind permission of Springer Science and Business Media.)

TABLE 10.2. Summary Analysis of Variance findings for simulated landscapes evaluated in a 9×9 factorial experiment with nine levels of habitat abundance (10–90%) and nine levels of fragmentation (0.1–0.9) above and below a persistence threshold (see Figure 10.5). DF= degrees of freedom.

Source of variation	*DF*	% of Total *SS*	*F*	*P*
Full experiment				
Habitat amount	8	96.8	15,871.5	0.0001
Fragmentation	8	0.7	124.4	0.0001
Habitat amount × fragmentation	64	0.6	13.3	0.0001
Error	2,349	1.8	–	–
Above threshold				
Habitat amount	6	96.3	10,497.2	0.0001
Fragmentation	8	0.7	55.8	0.0001
Habitat amount × fragmentation	42	0.5	8.3	0.0001
Error	1,653	2.5	–	–
Below threshold				
Habitat amount	3	30.3	122.3	0.0001
Fragmentation	8	6.2	9.4	0.0001
Habitat amount × fragmentation	12	6.1	6.2	0.0001
Error	696	57.4	–	–

Source: Applying Landscape Ecology in Biological Conservation, 2002, p. 434, Prescribing Habitat Layouts: Analysis of Optimal Placement for Landscape Planning, C.H. Flather, M. Bevers, and J. Hof. Copyright 2002 Springer-Verlag, New York, Inc. With the kind permission of Springer Science and Business Media.

population persistence (Figure 10.5c). That is, the *amount* of habitat remained the critical variable in determing the *size* of the population at all levels of habitat availability, but the *arrangement* of habitat began to abruptly increase in importance if there was less than or equal to 40% habitat in the landscape. In this model, was $p_c = 0.4$?

In Flather et al.'s model, habitat loss and fragmentation had significant effects on populations. Because species abundance and diversity are often area dependent, both decline as the amount of habitat is reduced. The overall loss of habitat and the isolation of the patches can reduce population sizes to such low levels that indigenous species may become extinct in individual patches, or even in an entire group of patches (Gaines et al. 1997; Rosenberg et al. 1997). Population decline occurs through several mechanisms. Some species require home areas or breeding territories of minimum critical sizes. Although such critical sizes may vary according to the densities of needed resources, there will be some lower limit, below which the species cannot exist. When habitat fragmentation reaches the point that insufficient area remains for these species to maintain a breeding population, these species will be lost. Some species have low dispersive ability and cannot cross large areas of non-habitat to reach new areas of suitable habitat. Finally, small fragments are more likely to lose species over time because their small populations are more susceptible to extinction.

It is difficult to separate effects of habitat loss, fragmentation, and isolation because such events often occur together and their outcomes are confounded. Figure 10.6 displays these distinctions graphically. Note that in A the amount of habitat is reduced but the number of habitat patches remains constant. This scenario represents simple habitat loss, not fragmentation. In B two of the four patches are removed, but the two that persist remain constant in size. This is a case where fragmentation of the remaining habitat is actually decreased. In C, the four original habitat patches are broken into 14 smaller patches. Here, and only here, do we have a condition of habitat loss *and* habitat fragmentation. How do we determine the relative contribution of each effect to declines in populations and in the diversity of communities? If declines are due to habitat loss, then the goal of conservation is to prevent such loss and, if possible, add more habitat. If declines are due to fragmentation and isolation, the spatial arrangement and connectivity of patches becomes the primary concern. If we misdiagnose the problem, we will apply an inappropriate solution that will waste resources and effort. Models are useful, but endangered species do not live in computers. Are there cases where predictions of percolation theory are upheld? Two studies address this question directly. Both involve the poster species of conservation-development conflicts, the spotted owl.

10.3.3.2. The Spotted Owl: Population Predictions and Conservation Planning

The northern spotted owl (*Strix occidentalis caurina*) is an endangered subspecies that breeds primarily in old-growth forests in the US Pacific Northwest. Conservation scientists who have studied the biology of the owl, and in particular its reproductive ecology, were able to determine the dispersal distances of juvenile owls during the periods when they

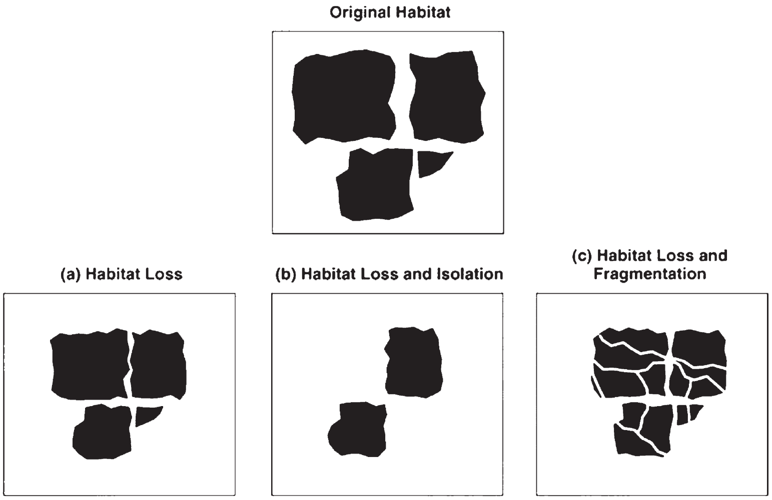

FIGURE 10.6. A conceptual illustration of habitat loss, fragmentation, and isolation. In situation (a), all patches are consistently smaller. In situation (b), habitat fragmentation is actually decreased because there are fewer patches. In situation (c), in addition to increasing patch separation, fragmentation decreases patch size. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

left their natal areas and traveled in search of new areas to establish breeding territories. Based on such investigations, scientists were able to construct a landscape-level model that could evaluate the probability of population persistence at different levels of habitat availability (old growth forests), using movement rules determined from actual dispersal abilities of juvenile owls. After conducting repeated simulation experiments, the researchers came to a disturbing conclusion. Sharp extinction thresholds appeared at the point where old-growth habitat was reduced to ~20% of the landscape. At that level, using the previously described movement rules, the ability of juveniles to locate suitable territories became compromised, leading eventually to population extinction. These results led to recommendations for the following habitat design criteria: individual habitat areas should be large enough to support at least 20 breeding pairs; habitat areas should be no farther than 19 km apart; and the matrix between habitat areas should be 50% forested with tree diameters >28 cm and with canopy closure >40% to facilitate juvenile dispersal (Noon and McKelvey 1996).

Notice how closely the findings of this species-specific model parallel the findings of the model developed by Flather et al., and how closely such findings match the predictions of percolation theory. But also notice that the amount of habitat recommended in reserve design was close to the theoretical persistence threshold defined by the model. What would happen to owl populations if there was a catastrophic event that reduced habitat availability *below* 20%? This was a stochastic model, and its outcomes reflect uncertainties specified within a defined range of probabilities for demographic and environmental events. Suppose, within that uncertainty, that a given period of time proved to be "unusually unlucky" for owls in terms of demographic and environmental stochasticity. Living on the edge of their persistence threshold of 20% available habitat, a "series of unfortunate events" in demographic or environmental stochasticity could send the population "over the edge" into extinction.

In cases where habitats harbor resources of high value to humans, such as timber in an old growth forest, final conservation plans may be determined as much by political processes as scientific modeling, in which case concerns about persistence thresholds and percolation theory are ignored. But important insights from such modeling must not be lost. The model by Flather et al. and Fahrig both suggest that, where habitat loss is substantial, effects of fragmentation become significant to population persistence, and such effects will occur suddenly when the "persistence threshold" is attained, although the exact level of that threshold is difficult to determine and varies by species. When that threshold is reached, fragmentation and isolation do matter, and conservation efforts to achieve optimal arrangement of remaining habitats become important. The northern spotted owl provides an example in which a species-specific habitat suitability model, developed from actual field studies, made predictions and generated outcomes consistent with those of percolation theory. But can percolation theory be applied in the planning stages of a conservation effort, such as a species recovery plan?

One such application is the inclusion of a percolation-based analysis of habitat connectivity in the recovery plan for the northern spotted owl's taxonomic cousin, the Mexican spotted owl (*Strix occidentalis lucida*) (Keitt et al. 1995). In addition to assessing habitat connectivity, this application of percolation theory led to the identification of critical habitat patches that were essential for the maintenance of landscape connectivity. Assuming a maximum dispersal range of 45 km for juvenile owls, the connectivity of forested habitat in this region is tenuous, at best (Figure 10.7a). At this critical dispersal distance, only one patch linked the southwestern and northeastern parts of its range, the old growth forests of the US Forest Service's Mount Taylor Ranger District of the Cibola National Forest in central New Mexico (Figure 10.7b). Analysis revealed that the Mount Taylor Ranger District was, in fact, a crucial stepping stone that connected owl populations in Arizona

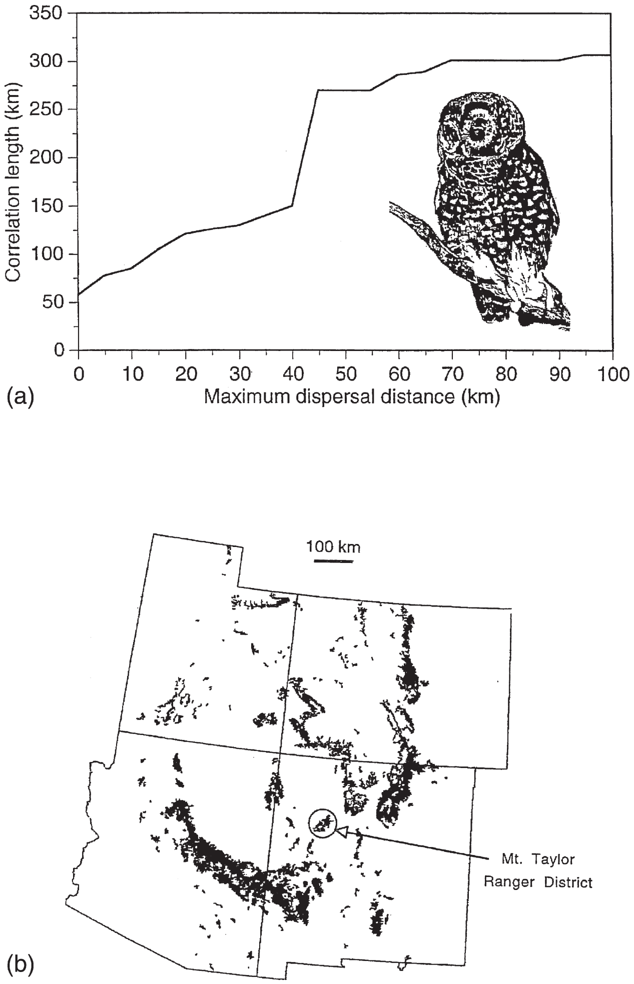

FIGURE 10.7. (a) Relationship of maximum dispersal distance (km) of the Mexican spotted owl (*Strix occidentalis lucida*), and "correlation length," or "connectivity distance" (km), the maximum distance between "connected" habitats. Note that at dispersal distances below 45 km (the maximum estimated dispersal range for juvenile owls), connectivity distance drops sharply, indicating that, to owls, available habitats separated by more than 150 km from one another are effectively "disconnected." (b) Location and strategic importance of the Mount Taylor Ranger District in central New Mexico (USA). Although having a low number of Mexican spotted owls, the Mount Taylor Ranger District is the critical "stepping stone" creating connectivity of habitats for owls in the four state area of Utah, Colorado, Arizona, and New Mexico, without which the northeastern and southwestern populations lose connectivity with one another. (With 2002a. Copyright 2002 Springer-Verlag, New York, Inc. With the kind permission of Springer Science and Business Media.)

and New Mexico to those in Colorado and Utah. This was not obvious prior to the analysis of landscape connectivity. In fact, the Mount Taylor District had previously been considered unimportant habitat because it supported so few resident Mexican spotted owls.

10.3.4. Field and Experimental Studies of Habitat Fragmentation

Percolation theory provides a framework for understanding some of the reasons why habitat fragmentation leads to population decline, and why habitat connectivity is important to population persistence, but its specific predictions can be difficult to test in the field. However, broader effects of habitat fragmentation can be effectively investigated, and need to be. Although habitat fragmentation is hypothesized to be the cause of population decline in many species, careful experiments are needed to determine if such a hypothesis is valid. Fortunately, there are studies that shed light on these effects.

In a formerly forested area of Australia now fragmented by agriculture, the size of remaining forest patches proved to be the best predictor of species richness of terrestrial mammals (Bennett 1987). Here, the effects of habitat fragmentation on small mammal communities have been especially well documented (Bennett 1990). First, among eight investigated species, six native and two introduced, the introduced black rat (*Rattus rattus*) and house mouse (*Mus musculus*) proved much more tolerant of fragmentation than the native species. The introduced species were more common in small forest fragments (2–10 ha) than larger fragments (20–80 ha). Native species were less tolerant of fragmentation, occurring less frequently in smaller fragments than larger ones.

Larger fragments consistently had more species, the frequency of occurrence of native species consistently increased in samples of larger-sized fragments, and the pattern of increase followed a predictable sequence. For example, four species occurred in over 50% of fragments 41–100 ha in size, but no species occurred in over 50% of fragments less than 2 ha in size. Two bandicoot species (*Isoodon obesulus* and *Perameles nasuta*) were rarely found in fragments smaller than 40 ha, and the long-nosed potoroo (*Potorous tridactylus*) was rarely found in fragments smaller than 8 ha. The view that fragmentation leads to smaller populations was borne out in this study. The bandicoots, which used only larger fragments, were of special concern because, even in the larger fragments, their populations were extremely small (Bennett 1990).

Different species respond differently to fragmentation. In the Australian study, variation in body size among species explained 83% of their variation in tolerance to fragmentation. The larger the average body weight of the species, the lower its tolerance. This pattern also has appeared in studies of small mammals in other areas. Diffendorfer et al. (1995) examined the effect of habitat fragmentation on three species of North American grassland rodents, the hispid cotton rat (*Sigmodon hispidus*), the prairie vole (*Microtus ochrogaster*) and the deer mouse (*Peromyscus maniculatus*), by experimentally fragmenting grassland habitat to varying degrees. The largest of these, the cotton rat, had higher densities in contiguous habitat, but the two smaller species had higher densities in fragmented habitat. The smallest species, the deer mouse, had the most positive response to fragmentation, was most abundant in the smallest areas, and used the interstitial areas that were created to separate habitats. Diffendorfer et al. (1995) believed that these differences arose from a combination of differences in habitat quality and changes in competitive interactions. The cotton rat suffered from habitat fragmentation because smaller sites had insufficient resources for long-term survival. Its decline in fragmented habitats created competitor-free space for the two smaller species. The deer mouse had the most positive response because the greater the degree of fragmentation, the greater the area of interstitial border areas, which it could use as well as the original habitat. For this species, fragmentation increased the amount of habitat available.

Bennett demonstrated differences in tolerances to fragmentation based on species occurrence. Diffendorfer et al. offered hypotheses about the mechanisms through which fragmentation created differences in species abundance. Can we go further, and isolate the effects of habitat loss, habitat fragmentation, and edge influences on real populations?

10.3.5. Habitat Loss and Fragmentation: Experimental Isolation of Separate Effects

Perhaps one of the most ingenious field experiments on the problem of habitat loss and fragmentation was designed by Samuel Marshall, Sean Walker, and Ann Rypstra, biologists at Miami University in Ohio (USA). These scientists were increasingly concerned that the effects of habitat loss, habitat connectivity (fragmentation), and the degradation of habitats within the interior of a habitat patch ("interior habitats") due to edge influences were too often confounded in conservation studies, such that, even when a significant effect was observed on affected populations, it was impossible to determine exactly which process was actually causing the effect. As Marshall and his colleagues noted, "Part of the challenge in studying the mechanisms behind the influence of habitat fragmentation on species persistence is that the spatial and ecological attributes of fragmented landscapes have correlated effects. … For example, fragmented landscapes generally suffer a net loss of habitat in addition to increasing spatial subdivision leading to an overall decrease in connectivity and core habitats" (Marshall et al. 2006:241). Further, such studies often have assumed that species with certain ecological traits like large home range size, habitat specialization, and aversion to edges (i.e. "interior" species) will suffer more from habitat loss, fragmentation (connectivity) and edge influence, and species with the opposite suite of traits will suffer less, or even benefit from it. But the charactetiztation of some species as "interior species" or "edge species" has often been made with little empirical support, and rarely have these readily accepted generalizations been carefully investigated.

To isolate these correlated but distinct effects, Marshall and his colleagues examined the effect of landscape pattern on populations of two species of wolf spider, *Pardosa milvina* and *Hogna helluo*. Wolf spiders are vagrant, generalist invertebrate predators that hunt their prey on the surface of soils. Because they dwell almost exclusively on the surface they are sensitive to changes in soil-surface conditions, especially moisture and temperature. The major determinants of soil moisture and temperature are the frequency of disturbance and the accumulation of vegetative litter. Of the two species, *Hogna helluo* (Figure 10.8) is larger, more habitat selective, a poor disperser, and averse to bare (i.e. disturbed) surfaces. In contrast, *Pardosa milvina* is smaller, more vagile, and will make use of barren (disturbed) surfaces. But how could one create habitats in which habitat loss, habitat fragmentation, and habitat isolation could be manipulated independently in these species?

Marshall and his colleagues solved the problem by using a pre-existing experimental field, formerly used to grow soybeans, that had been converted to conservation tillage, thus producing a habitat more like a native North American prairie, with increased densities of vegetation, a change that produced an increase in the densities of wolf spiders. Using arrays of 25 2 × 2 m habitat cells ("habitat islands") in multiple field plots, they randomly selected either 5 (20%) or 20 (80%) of the cells in each

FIGURE 10.8. *Hogna helluo*, a large, habitat selective species of wolf spider with poor dispersal ability and aversion to habitat disturbance, experiences population declines when subjected to habitat fragmentation. (Photo courtesy of Samuel D. Marshall. Used by permission.)

array for destruction with one array left undisturbed as a control. Then, in a separate experiment to isolate the effect of fragmentation, they divided a 25 m^2 area into two, four, and eight equally spaced squares, while keeping a separate single 25 m^2 patch undivided to represent a least-fragmented habitat. In the subdivided areas, subdivision carried out in this way would keep the total amount of habitat constant but increase its fragmentation. Finally, to isolate the effects of edge influences, they created three different landscape configurations in the field: (1) square, 5 × 5 m; (2) rectangle, 7.5 × 3.3 m; and long rectangle, 10 × 2.5 m (Marshall et al. 2006:243–244) (Figure 10.9). By creating habitats of different shapes, Marshall et al. changed the amount of edge without changing the amount of habitat. In their own words, this is what happened.

"There was a strongly opposing response to habitat destruction by the two wolf spider species. Population densities of *Hogna* declined by approximately 75% with only a 20% reduction in area, while *Pardosa* numbers are almost twice as high in the 80% area reduction treatments as in the no-destruction controls" (Marshall et al. 2006:244). Thus, habitat loss, independent of isolation or fragmentation, had greater effect on *Hogna*, the "interior" species, than on *Pardosa*, the "edge" species. Further, "There was a negative response by *Hogna* populations to the increasing subdivision of the habitat … and no significant response to habitat fragmentation by *Pardosa*." (Figure 10.10) and "*Hogna* populations had a negative response to increasing edge in the subplots …, whereas *Pardosa* was apparently unaffected…" (Figure 10.11) (Marshall et al. 2006:245). Thus, habitat loss, habitat fragmentation, and increased edge independently produced negative effects on *Hogna*, but not on *Pardosa*.

FIGURE 10.9. Aerial photograph of the experimental fields near Miami University, Ohio (USA) used in the study of responses of two species of wolf spider *Hogna helluo* and *Pardosa milvina* to habitat fragmentation. Each field is 60 × 70 m and holds a replicate of either an area reduction experiment (fields with three large subplots) or of an area subdivision experiment (fields holding four subplots). (Photo courtesy of Samuel D. Marshall; Marshall et al. 2006. Two ecologically-divergent generalist predators have different responses to landscape fragmentation, *Oikos*, Copyright 2006 by Blackwell Publishing.)

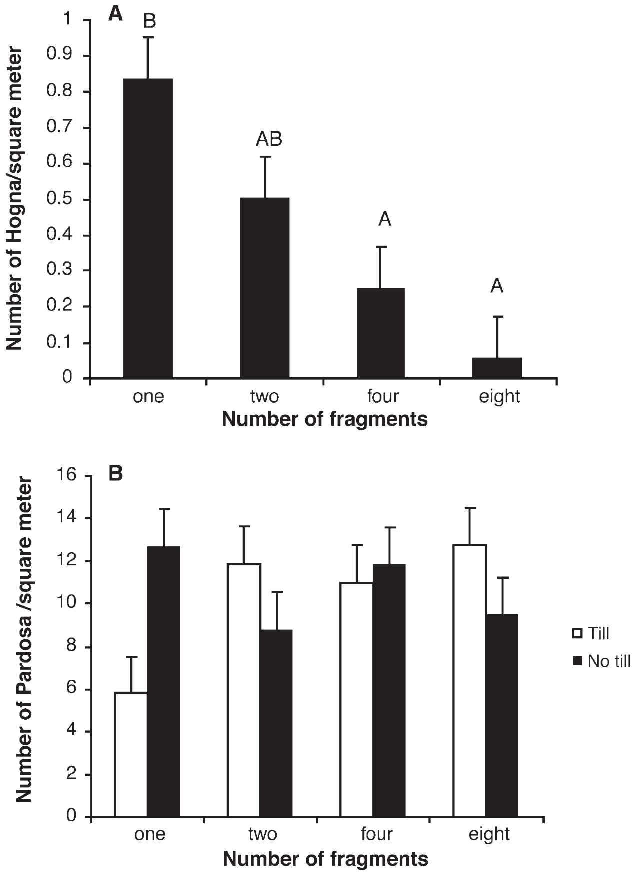

FIGURE 10.10. (A) Response of *Hogna helluo*, a species of wolf spider favoring specialized "interior" habitat conditions, and (B) *Pardosa milvina*, a smaller, more mobile species of wolf spider tolerant of disturbed conditions, to increasing habitat subdivision (fragmentation) in an experimentally manipulated field environment. Error bars represent standard error of the mean. (Marshall et al. 2006. Two ecologically-divergent generalist predators have different responses to landscape fragmentation, *Oikos*, Copyright 2006 by Blackwell Publishing.)

Recall that neutral landscape models tend to treat cells in the landscape as either hospitable habitat, which can be occupied by an organism, or as an inhospitable "matrix" of non-habitat that organisms cannot maintain residence in. Based on their study, Marshall et al. offer interesting insights into this traditional perspective. "… 'the matrix' is generally assumed to be inhospitable to the focal species and if this assumption is false it will lead to misinterpretation of experimental results. We propose that the same barren habitats that function as an aversive matrix for *Hogna* (i.e., functionally inhospitable) may be a useful, and even necessary, landscape element for *Pardosa*.… *Hogna* and *Pardosa* present a revealing contrast of how two related, syntopic species will respond to habitat fragmentation as a result of their divergent ecologies. The very different responses of *Hogna* and *Pardosa* to landscape fragmentation are entirely consistent with what we know about

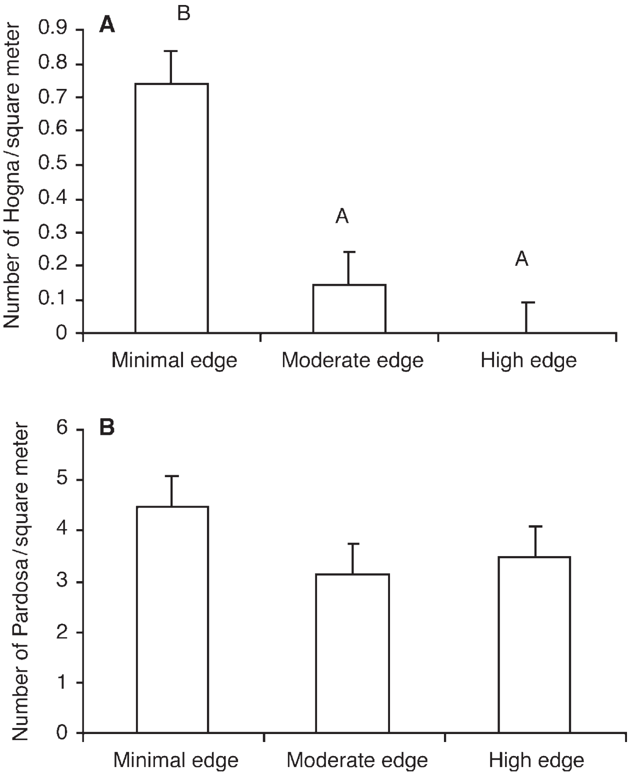

FIGURE 10.11. (A) Response of *Hogna helluo*, a species of wolf spider favoring specialized "interior" habitat conditions, and (B) *Pardosa milvina*, a smaller, more mobile species of wolf spider tolerant of disturbed conditions, to increasing ratios of ratios of edge to interior habitat in an experimentally manipulated field environment. Error bars represent standard error of the mean. (Marshall et al. 2006. Two ecologically-divergent generalist predators have different responses to landscape fragmentation, *Oikos*, Copyright 2006 by Blackwell Publishing.)

their very different ecology and behavior" (Marshall et al. 2006:247). Thus, whether terms like "edge species" or "interior species" ultimately prove useful to science, Marshall et al. succeeded in experimentally demonstrating that the effects of habitat loss and habitat fragmention have different effects on different species, even species that are closely related, and such effects can have significant population consequences.

10.4. Life on the Edge – Edge Effects Lead to Habitat Degradation

10.4.1. Understanding the Effects of Edge: First Principles

Thus far we have focused on the overall effects of habitat loss and fragmentation and their effects on population persistence, especially in the context of habitat connectivity. But, to effectively conserve habitat and the species a habitat contains, we must understand the specific effects created and the processes altered when the phenomenon of ***habitat edge*** is increased in a landscape. Any degree of habitat fragmentation usually has a far greater effect on species dependent on conditions unique to one habitat like *Hogna helluo* than on so-called "edge species" (species that are adapted to habitat borders) like *Pardosa milvina*. Habitat fragmentation can, under certain conditions, actually increase the amount of habitat for edge species. Consider a forest in which 40% of original habitat in a single block is destroyed and the remainder exists as two blocks (Figure 10.12). In this case, edge species suffer no loss of habitat, but interior species lose 60% of their habitat. Given the pronounced effect of habitat fragmentation on a habitat patch's area-to-edge ratio, it is not surprising that some of the most well known and well-studied aspects of habitat fragmentation are ***edge effects***.

What happens when a habitat is fragmented? Begin with a 1 km^2 (100 ha) block of contiguous habitat (Figure 10.13). Assume that changes associated with edges penetrate 100 m at each border and are the same on all sides. This reduces the amount of "core" habitat (habitat unaffected by edge effects and processes) to an area 800 m long and 800 m wide, or 64 ha. Now bisect this block by one road and one power line. Assuming that 10 × 100 m are lost for the power line and its right of way (1,000 m^2), 10 × 100 m are lost by the space taken up by the road (1,000 m^2), and that edge effects continue to penetrate 100 m at each boundary, the habitat unaffected by edge is reduced from a single block of 64 ha to four separate blocks, each 295 m on each side, or 8.7 ha in area. The four blocks now contribute only 34.8 ha of habitat unaffected by edge effects, little more than half (54%) of the unaffected habitat present in the original block.

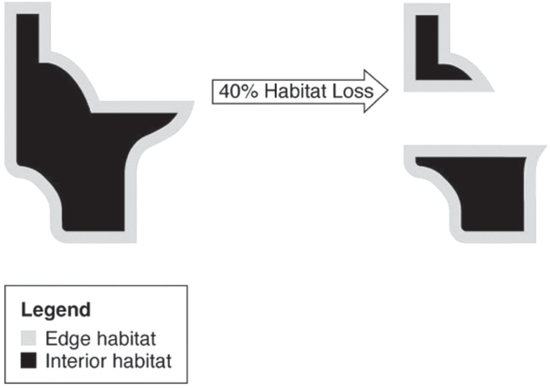

FIGURE 10.12. The effect of habitat loss on amounts of edge and interior habitat. When a 40% portion of habitat is removed, the amount of interior habitat decreases by approximately 60%. In this scenario edge species do not experience a significant increase or decrease in habitat. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

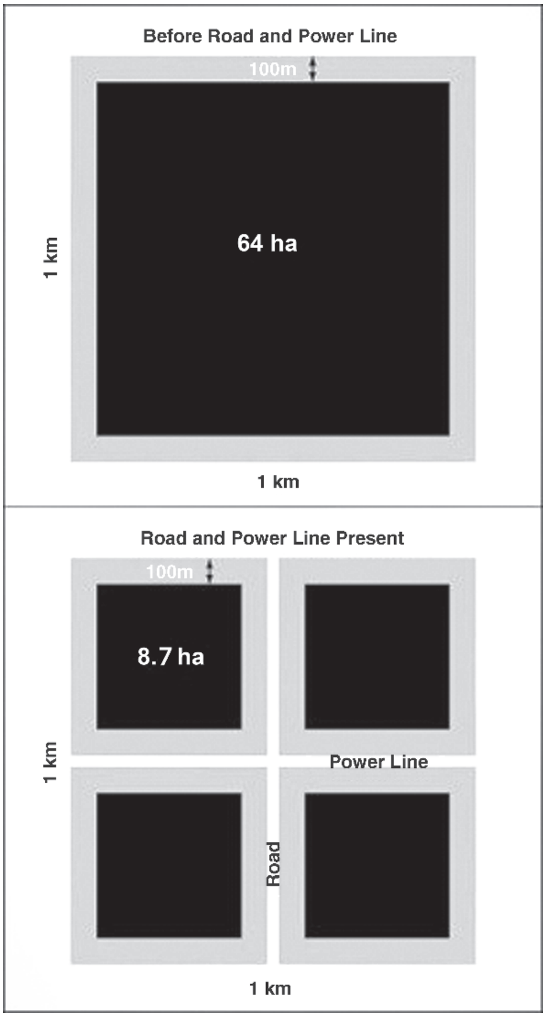

FIGURE 10.13. The effect of habitat fragmentation on edge and interior habitat. Note, in this scenario, when a road and power line intersect the habitat, edge species experience a net habitat increase of over 80%, while interior species lose nearly 50% of their original habitat.

This example illustrates two principles. First, as long as fragmentation continues, edge habitat increases and core habitat decreases. Second, in the early stages of fragmentation, core habitat is moved closer to edge habitat and to the processes and effects associated with the edge environment. From this understanding, we can examine the details of edge effects with more precision and gain more insight as to why increasing the amount of habitat exposed to edge can have the same effect as direct habitat loss.

10.4.2. Edge Influence: Understanding Processes and Effects

Edge effects are complex and highly variable, and will change according to time, variables studied, edge orientation, management history, and many other factors. Despite the great diversity of form and effect that characterize edges, all edges share at least two commonalities: exchange or flow of energy, material, and/or organisms across the boundary and alterations in biophysical processes and ecosystem composition and structure. Analytically, the degree of edge influence (EI) will be determined by three things. The first is a quality that is known as "patch contrast." Specifically, the greater the differences between the two habitats forming the edge, the greater is likely to be the effect of edge influences on both habitats. Flows of energy across an edge increase with greater patch contrast, and such flows regulate the magnitude and distance of edge influences into interior habitat. Habitat managers generally believe that edge influence can be minimized by reducing the contrast between patches. For example, in a forest, reducing contrasts between age or structure of adjacent forest stands is recommended to reduce edge influences (Harris 1984).

A second determinant of edge influences is the rate of dissipation of the edge effect over distance from the edge into the interior of the habitat. This "distance effect" is sometimes incorporated into models that attempt to simulate the effects of edge influences, in which case it is sometimes referred as the "decay value," designated as *K*. Daolan Zheng and Jiquan Chen developed a model for measuring edge effects in forest environments in which they specified decay values for different variables (Zheng and Chen 2000). In their model, the decay value would determine the rate of change from a clearcut to the interior forest for a specific variable such as, for example, wind speed. The larger the decay value, the faster the variable changes per unit distance from the edge. In other words, large decay values would be associated with rapid change in the value of the variable over a short distance, while low values would indicate little change over a long distance (Figure 10.14). Individual *K* values can vary significantly from one variable to another. For example, at a forest-clearcut edge, windspeed might change from 40 kph at the edge to 10 kph 20 m from the edge, a decay value that could be expressed as −30 kph/20 m or, more basically, −1.5 kph/m.

A third determinant of the effect of edge influences is that of magnitude or strength of the edge influence. To remain with our example of wind effects, magnitude could be estimated as the speed of the wind at the edge, which might vary from 40 kph at the edge of a forest – clearcut boundary to <5 kph at a boundary between two different kinds of forest of similar ages and structures. Decay and magnitude can vary independently in the same variable and will not necessarily respond to edge creation in the same way. The relationship between decay and magnitude could be envisioned as a gradient that could vary from steep and short (a variable of high magnitude that loses its effect over a short distance) to shallow and long (a variable of low magnitude that retains its effects deep into the interior of the habitat (Zheng and Chen 2000).

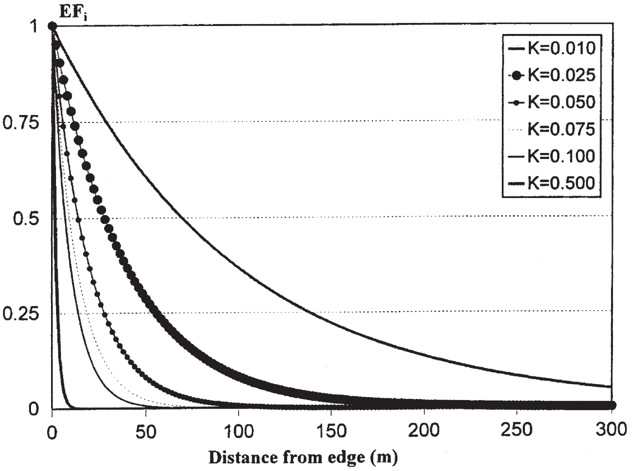

FIGURE 10.14. Theoretical relationships between magnitude of edge factors and distance from edge as functions of decay values (*K*) in a forest landscape. Variables with high values of *K* are associated with edge effects that decay quickly over a short distance into the forest. Variables with low *K* values are effects whose influence declines slowly over a long distance. (Zheng and Chen 2000. Copyright 2000. With permission from Elsevier.)

Effects that are influenced by patch contrast and can be measured by decay and magnitude can be classed as "primary" or "secondary" effects of edge influence, sometimes referred to as "direct" or "indirect" effects. Primary responses are those resulting immediately and directly from the effects of edge creation. To remain with our forest scenario, primary process responses could include damage to trees and other vegetation; disruption of the forest floor and soil; increased dispersal of pollen and seeds; changes in evapotranspiration, nutrient cycling, decomposition, and rates of energy exchange. These ecological processes are then mechanisms responsible for primary structural responses such as changes in forest structure (including canopy cover, tree density, downed wood, leaf area, and vegetative biomass). Subsequently, secondary responses arise because the primary responses change the original abiotic and biotic gradients associated with the edge. Secondary processes to edge creation such as, in vegetation, regeneration, growth, reproduction, and mortality, reflect both edge-related gradients and primary responses to them. As edges age, they may be subject to processes such as sealing, softening, or expansion. "Sealing" refers to the development of dense vegetation at the edge, an effect especially pronounced at maintained edges. "Softening" is the reduction of edge influence at regenerating edges. "Expansion" refers to increase in extent of edge influence over time (Figure 10.15) (Harper et al. 2005).

All edges are characterized by distinct abiotic and biotic gradients associated with these effects. Flows across edges driven by these gradients have been likened to movement across a semipermeable membrance. Consider a common direct effect of edge creation in a forest, tree damage. Tree damage leads to reduced canopy cover and greater abundance of snags and logs at edges. In this case, the primary process response of tree mortality has greater magnitude and distance of EI than the primary structure response. Following primary edge responses, accentuation of abiotic gradients near edges is the probable mechanism for secondary process vegetation responses of regeneration, growth, and mortality. These secondary processes often have distance and magnitude similar to or greater than primary responses, probably because primary structural responses initiate secondary responses that occur farther from the edge (Harper et al. 2005).

There are situations in which edge influence is more pronounced and more ecologically important, other conditions being equal. These are: (1) high mean annual (or growing season) air temperature, (2) low latitudes with high solar radiation, (3) low mean annual (or growing season) cloud cover, (4) frequent, extreme winds, (5) edges facing the equator or into prevailing winds, (6) shallow soil depth, (7) abrupt, open edges, (8) edges where patch contrast is maintained over time, (9) forests with tall, dense canopies, (10) closed-canopy (generally mid-successional or mature) stands, (11) regional flora or fauna with many pioneer species, (12) regional flora or fauna with many exotic and invasive species, (13) biomes or forest types subject to infrequent stand-replacing disturbances, or (14) forest communities or landscapes with low inherent heterogeneity in vegetation, topography, or soils. When managers work to conserve biodiversity under these conditions, they must be particularly concerned with how to mitigate edge influences.

10.4.3. Environmental Characteristics of Edges

Once edge influences are in play, the associated effects and processes can create an environment with very different characteristics than the associated interior habitat. Many of these differences are physical and obvious. Edges usually receive more direct insolation, and thus are typically warmer and have lower relative humidity than interior areas, especially in forest habitats. Radiation and moisture fluxes are greater at edges. Increased radiation and insolation at edges tend to increase soil temperatures and affect rates of invertebrate and microbial activity (Klein 1989; Parker 1989) and associated processes of nutrient decomposition. Increased soil temperatures may also reduce the retention of water in the soil and alter the growth rates and phenology of vegetation.

Wind behaves differently at edges than in the interior of a habitat. As wind moves over a landscape and flows from one type of vegetation to another, the upper part of the wind profile retains the characteristics formed over the previous vegetation type, while the lower portion takes on the profile characteristics of the new vegetation. The two profiles do

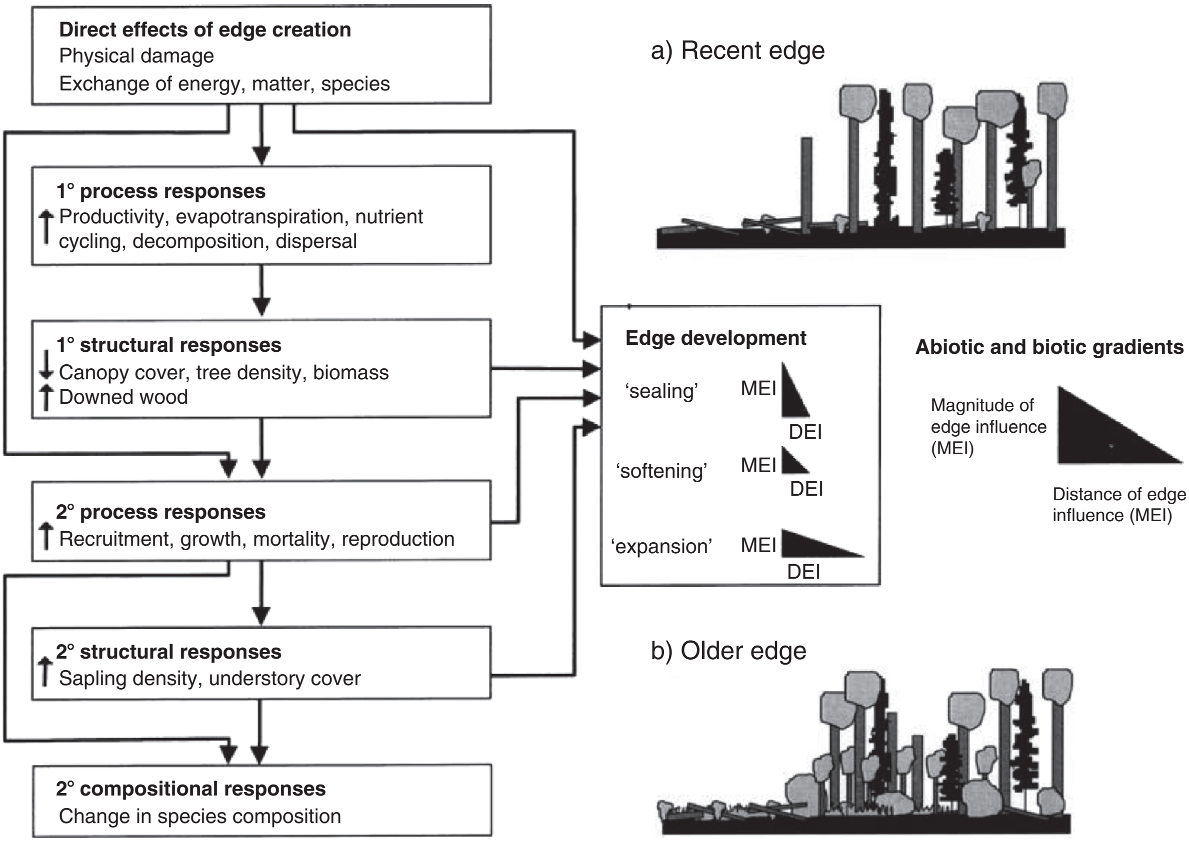

FIGURE 10.15. Conceptualized diagram of processes and responses following edge creation including (a) a recently created edge and (b) an older edge. Upward and downward arrows within boxes denote increases and decreases, respectively. Abiotic and biotic gradients (triangles, with height representing magnitude of edge influence (MEI) and length representing distance of edge influence (DEI)) are strong at newly created edges and become steeper, weaker, or longer at older edges with edge sealing, softening, or expansion. Edge sealing is the development of dense vegetation at maintained edges. Edge softening is the reduction of edge influence at regenerating edges, and edge expansion is the increase in extent of edge influence over time. (Harper et al. Edge influence on forest structure and composition in fragmented landscapes, *Conservation Biology*, Copyright 2005 by Blackwell Publishing.)

not fully equilibrate with one another for some distance, increasing turbulence and wind shear at their boundaries. The distance required for equilibration is normally four to six times the height of the vegetation. The effects of edge on wind behavior have important consequences. Trees near an edge are more susceptible to damage, wind pruning, uprooting, and other forms of physical damage. Increased wind speeds also can lead to increased evapotranspiration and desiccation. Secondary effects of wind at edges can include increased transport of material into the interior from surrounding, but different, vegetation types, including soil, seeds, insects and dead organic matter.

Habitat fragmentation and its associated creation of edge also alters local water regimes. Rates of interception and evapotranspiration are changed by removal of native vegetation and by modification of native vegetation at the edges of remnants (Saunders et al. 1995). Replacement of deep-rooted perennials, which are more typical of native vegetation, with herbaceous crops, pasture, or non-vegetative surfaces at edges leads to greater runoff and increased surface and groundwater flows, with accompanying increases in rates of erosion and transport of particulate matter.

Other characteristics of edges are manifested as biological phenomena because biological interactions also change at edges, usually to the detriment of species adapted to interior habitats. Many studies have shown that edge habitats create a variety of detrimental effects on interior species of both plants and animals, including increased predation, increased parasitism and increased herbivory (Laudenslayer 1986; Alverson et al. 1988; Harris 1988; Temple and Cary 1988; Yahner 1988). For example, the presence of edges can alter and intensify interspecific interactions. Some generalist mammalian predators, such as northern raccoon (*Procyon lotor*) and red fox are known to preferentially follow edges rather than forage in interior habitat areas. Some bird species common to edges, such as blue jays (*Cyanocitta cristata*) and house wrens may engage in nest predation (blue jays) or the destruction of eggs of other species (house wrens).

Increased edge results in less secure habitat for interior species (Temple 1986) because nest predators and parasites not only reduce their nesting success at edges, but penetrate more deeply into the interior of other habitats from edges. For example, increased rates of nest predation among forest birds may extend up to 600 m into the forest from the edge (Wilcove 1985). Thus, there is less habitat in which resident species are unaffected by edge processes and effects. Predators associated with edges of habitats have characteristic "penetration depths" into blocks of homogeneous habitat. When habitat is fragmented and the ratio of edge-to-interior increases, species dependent on particular habitats become more vulnerable to predation because they have little habitat left that edge predators cannot penetrate. In North America, species of insectivorous songbirds with high vulnerability to predation during the breeding season have declined significantly in recent years, while those species with low vulnerability to predation during the breeding season have increased (Robinson et al. 1995). This finding has led some to conclude that habitat fragmentation and edge creation in temperate forests, with associated increases in penetration depths of predators, may be more important in songbird declines than the more publicized problem of tropical deforestation.

10.5. Managing Habitat Connectivity: The Role of Corridors in Habitat Conservation

10.5.1. The Theoretical Basis of Habitat Corridors

Percolation theory predicts that the key variable for successful habitat conservation, and their associated populations, is habitat connectivity. But habitat connectivity is disrupted by habitat fragmentation which, when it reaches a critical threshold, qualitatively changing the habitat from a connected to a disconnected state. Remaining fragments thus become increasingly vulnerable to the edge influences just described. The best conservation strategy is to prevent fragmentation. But that is no solution in habitats that are already fragmented, or where the best available habitat left to preserve is itself only a scattered array of isolated fragments.

Connectivity is a parameter of landscape function that measures the processes by which subpopulations of organisms are interconnected into a functional demographic unit (Merriam 1984). A related concept is connectedness. ***Connectedness*** refers to a physical linkage between landscape elements. Recall from Chapter 6 the critical role that connectedness and connectivity play in facilitating gene flow, dispersal, and colonization, particularly in metapopulations that exist as spatially discrete subunits. Although connectedness is necessary for populations to achieve connectivity, connectedness does not guarantee connectivity. Connectivity is achieved only if individuals actually move between connected units (Figure 10.16). If they do not, connectedness does nothing to increase the persistence of the population.

Habitat corridors are often proposed as a means of linking isolated reserves or fragmented patches of habitat. A ***corridor*** is *a linear landscape element that provides for movement between habitat patches* (Rosenberg et al. 1997) or *landscape structures that enhance the dispersal of organisms between suitable habitat patches in fragmented landscapes where isolates of suitable habitat are surrounded by a matrix of inhospitable habitat types* (Vos et al. 2002:84). These definitions have structural and functional components. The structural component is that corridors are linear and differ from their surroundings. The functional component is that dispersal from source habitats to target habitat occurs through the corridor. Thus, corridors are intended to aid dispersal and contribute to *functional connectivity* of a landscape.

The concept of connecting fragments of habitat with corridors originally arose out of predictions of reserve design derived from the theory of island biogeography (MacArthur and Wilson 1967). The belief was that corridors would provide avenues of movement and immigration between patches of habitat, leading to increased stability of populations in remaining fragments. Unfortunately, the appeal and plausibility of corridors often have outpaced definitive studies and rigorous interpretations needed to assess their actual role and value. Most advocates of corridors assert that: (1) animals will make use of corridors to move from one fragment of habitat to another; (2) fragments of habitat connected by corridors will have higher levels of species diversity than isolated fragments; (3) populations in fragments connected by corridors will have lower rates of species replacement (species turnover, a measure of community stability) than isolated populations; and (4) populations connected by corridors will have higher population densities, higher growth rates, and longer persistence times than populations in similar, but isolated habitats. These assertions are not always supported by data. To understand the role of corridors in conservation, studies of corridors must be correctly interpreted, and their insights applied to problems of reserve design.

10.5.2. Experimental Studies of Corridors

Confusion about the definition of corridors often leads to errors of interpretation associated with the experimental studies of corridors. In fact, relatively few studies have demonstrated that corridors actually provide connectivity; that is, increase the rate of successful

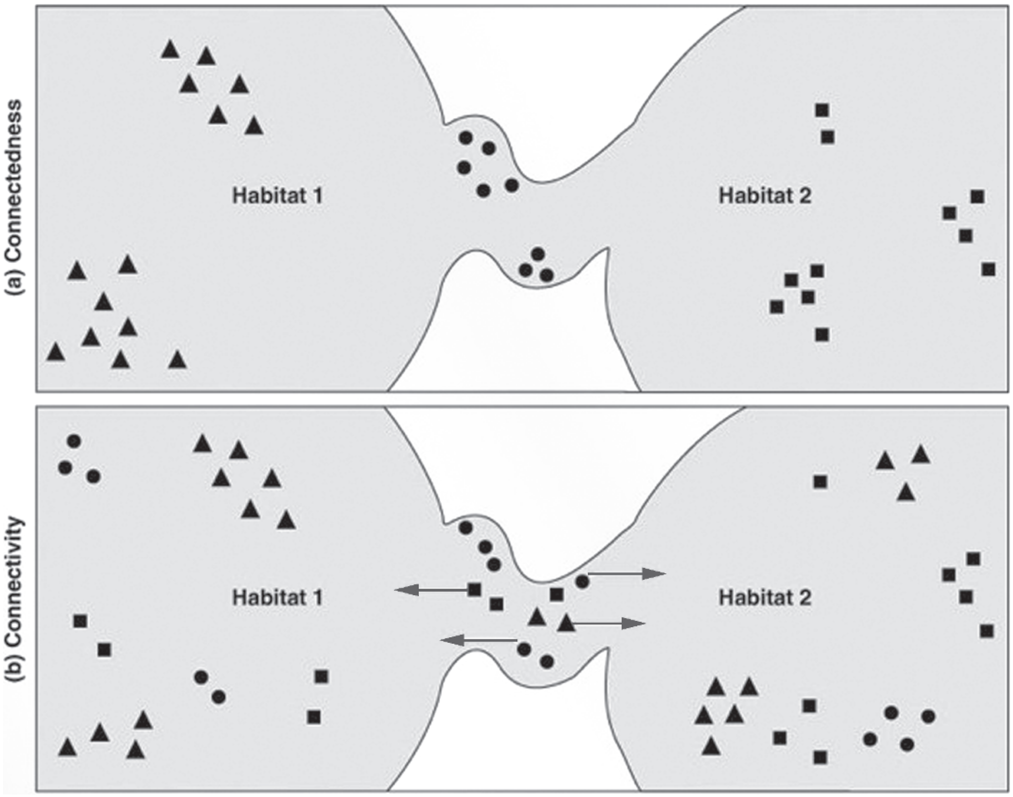

FIGURE 10.16. A conceptual illustration of the difference between connectedness and connectivity. Corridors create connectedness, but only movement of individuals from one habitat patch to another creates connectivity. In (a), each species (represented by different symbols) occupies a distinct area and there is no movement through the corridor; however, one species (•) uses the corridor as habitat. In (b), individuals of all three species move through the corridor, creating connectivity between habitats. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

movement of animals between patches. Instead, most studies of corridors have documented the presence of animals in the corridor (a linear patch of habitat lying between larger patches) and have inferred that the linear patches were acting as corridors (Rosenberg et al. 1997). For example, Merriam and Lanoue (1990), in a study of the use of fence rows by the white-footed mouse, demonstrate that most of the movements and 90% of all activity by radio-tagged mice occurred in fence rows. The authors consistently refer to the fence rows as "corridors" rather than "habitat," implying that the mice were moving through the fence rows to other habitats, but they present no data to support this assumption.

Many studies of corridors have failed to demonstrate that corridors are, in fact, used for movement between habitat fragments. Of 36 research papers in the book *The Role of Corridors* (Saunders and Hobbs 1991), only 5 presented new data on animal movement in and through corridors. Of these five, only one gathered data on movement between habitat patches without corridors. Only three of the five studies concluded that corridors had a role in conserving a particular taxon (Simberloff et al. 1992). In an experimental study of the use of corridors by three species of small mammals, cotton mice (*Peromyscus gossypinus*), old-field mice (*P. polionotus*), and cotton rats, Mabry and Barrett documented that, in these species, the home range size and average distance moved by individuals with access to corridors was not different than individuals without access to corridors, suggesting that, in these species, individuals could move through the interpatch "matrix" as well as they could through a corridor of the same habitat as their primary habitat patch (Mabry and Barrett 2002).

Some studies have provided indirect evidence of movement through corridors to adjoining habitats. For example, Haas (1995) demonstrated that American robins were more likely to disperse between shelterwood habitat fragments connected by wooded corridors than to adjacent, equally distant, shelterwood stands that were not connected by wooded corridors. Dmowski and Kozakiewicz (1990) demonstrated that non-littoral species of birds living in a pine forest near a lake were more likely to visit and use the littoral zones of the lake connected to the forest by a shrub corridor than to visit equally distant littoral zones separated from the forest by an open meadow. These authors also demonstrated that movements of non-littoral (primarily forest) species to the littoral zone occurred mainly through the shrub corridor. In an even more definitive study involving the ringlet butterfly (*Aphantopus hyperantus*), a species common throughout much of Europe and Asia, Sutcliffe and Thomas (1996) examined the butterfly's use of habitat patches in isolated woodlots and open tracks connecting woodlots that have been reputed to be used as corridors. Using direct observations of marked butterflies and mark-recapture methods, they determined that the ringlet butterfly did use tracks as dispersal corridors to move from one habitat patch to another. One of the few studies that was successful in combining an examination of both the habitat and movement functions of corridors was the previously cited work of Bennett (1990) on populations of small mammals in Australia. Investigating eight species of small mammals, six native and two introduced, that used both forest fragments and corridors between the fragments, Bennett documented a number of key corridor functions and values. First, all species occurred in corridors, but use of corridors differed by species. Some species, such as the bush rat, were breeding residents in corridors, using the corridors as permanent habitat. Other species, such as the introduced house mouse and the native brown antechinus (*Antechinus stuartii*), were primarily transients who used the corridors for movements between fragments of forest habitat. Several species had approximately equal proportions of transient and resident animals in corridors, and several individuals of different species had home areas that encompassed portions of both the corridor and adjacent forest habitat. Even species and individuals using the corridors as transients followed a variety of movement patterns, some traversing the corridor from one forest fragment to another in a single movement, others moving between adjacent patches through an extended series of gradual movements (Bennett 1990).

Bennett's (1990) study illuminated a number of key points regarding corridors by demonstrating that corridors are actually used in dispersal and as permanent habitat, and that individual species differ in their use of and movement patterns within corridors. However, Bennett made no examination of dispersal movements by the same species outside of corridors. Thus, although all documented dispersal movements of the examined species occurred through corridors, no examination of dispersal without corridors was sought (Simberloff et al. 1992). This omission undermines the credibility of Bennett's study in demonstrating that corridors enhance dispersal in these species.

Despite the imperfections and limitations of these and other studies of corridor function, there is growing evidence that corridors can add value to linear landscape elements. But such studies also demonstrate that three important qualifiers are needed when discussing the value of corridors. First, the role of corridors in both animal movement and population persistence is complex. Simple generalizations, however intuitive and appealing, are unhelpful, possibly erroneous, and could lead to bad decisions in landscape management. Second, studies of corridors must include appropriate controls in the experimental design to determine if dispersal, survival and movement of animals through and within corridors is really any different than it would be without corridors. Third, the value of corridors differs according to species and landscape scale. These studies have demonstrated some specific values of corridors in connecting closely spaced fragments of habitats (typically less than 5 km between adjacent fragments), but more studies are needed to establish the value of corridors at large scales more appropriate to conserving the processes of functioning ecosystems, and the scale at which corridors have been proposed to link large reserve complexes (Hunter et al. 1988).

10.5.3. Potential Disadvantages of Corridors

Just as there can be positive values attained through linking habitat fragments through corridors, so there can be negative effects (Simberloff et al. 1992). Isolation of a population or its habitat is not always bad, particularly if the population or habitat is especially susceptible to environmental variation and disturbance. Because corridors connect habitat fragments, they have the potential to "import" negative effects from one fragment to another. Parasites or agents of disease may move more easily through corridors from one habitat fragment to another than they could between isolated fragments. Non-native species also may use corridors as routes of dispersal from fragment to fragment. Mortality, especially predation, may be heavier on individuals residing or dispersing within corridors because predators indigenous to other, surrounding habitats may be able to penetrate corridors more easily than remaining habitat fragments. This effect could make corridors population sinks that could actually have negative effects on the overall levels of populations in the region.

Corridors could have indirect negative effects on population processes. The persistence of a metapopulation is enhanced by the fact that population subunits are sometimes non-synchronous in their population demographics. That is, cyclic patterns of population increase and decrease are independent events in different subunits. Dispersal of individuals from different subunits through corridors can reduce or eliminate such independence, making the population subunits more vulnerable to regional environmental variation and its effects on population processes. Thus, an environmental event that affects only low-density populations would eliminate some subunits in an asynchronous population, but could reduce or eliminate all populations if subunits were synchronous. Another threat that corridors pose to basic population processes is the problem of habitat quality. If patches of habitat are connected by corridors that are similar in quality to the habitats they connect, then persistence of subpopulations in the connected habitats increases (Fahrig and Merriam 1985). But simulation modeling has demonstrated that, if the corridors are of lower quality habitat, dispersers suffer higher mortality in corridors and overall population levels decline (Henein and Merriam 1990). Such modeling is supported in one field study of mammals in a fragmented tropical forest where 42% of variations in species richness in different forest fragments were explained by the area of the fragment, and an additional 40% was explained the degree of isolation of the fragments and the quality of habitat in connecting corridors (Laurance 1995).

Many factors can contribute to corridors being of lower quality than the habitat patches they connect. Even if vegetation in corridors is identical to connected patches, typical corridor shape (long and narrow) tends to increase edge and associated edge effects of increased predation and parasitism on interior species within the corridor. Corridors also represent both opportunity costs. They must be purchased and managed to provide conservation value. Thus, acquiring and managing corridors is a decision **not** to purchase and manage additional habitat to enlarge existing reserves. The effectiveness of corridors will vary with species, and with the characteristics of the corridor, especially its complexity of vegetation structure, its length from fragment to fragment relative to the dispersal abilities of the species targeted for conservation, and its width. Unless these factors are considered, the purchase of corridors, and the effects they have on linking previously isolated fragments, may be counterproductive to conservation goals. Unless corridors lead to population connectivity, they confer no advantage, and are less beneficial than direct restoration of lost habitat. Regardless of the value corridors have, they are not a final solution. It is landscape and habitat conditions that put populations in jeopardy that must be corrected (Merriam 1995).

POINTS OF ENGAGEMENT – QUESTION 2

Describe an experiment that could demonstrate whether corridors create connectivity between habitat patches. What would be your hypothesis and experimental design?

10.6. Planning for Reserve Design

10.6.1. Algorithms of Reserve Design

The Nature Conservancy (TNC) is one of the world's most influential non-governmental organizations in conservation, administering the largest system of private nature reserves in the world, with holdings on six continents. The problem TNC and other conservation organizations like them desire to solve can be stated simply: how can we best locate reserve units on a landscape in such a way that they contain the largest possible number of biodiversity elements? The Nature Conservancy's procedure for planning and designing reserve systems that solve this problem provides an exemplary model. TNC follows a three-stage process of reserve system planning: (1) many sites are screened as potential reserves, (2) candidate sites are examined for their promise as part of a functional system of reserves, (3) individual reserve sites are established, managed, and monitored – a process that continues for the life of the reserve system (Urban 2002). How would a site merit consideration for step one? Selection criteria used by TNC are (1) *ecological uniqueness* – what is site's level of species richness, rarity, and endemism, or other ecological features of special concern; (2) *viability* – what is the likelihood that species would persist on this site if it were protected as a reserve; and (3) *threats* – what agents might reduce the long-term viability or value of the reserve. For example, development pressure or impacts from surrounding land often constitute the primary and most important threats to the viability and quality of a reserve in most countries. (4) *Feasibility* – what are relevant economic, sociological, and administrative factors related to likelihood that reserve could actually be acquired and protected. This is the "can we really do this" criterion. A site that is unaffordable, politically unavailable, or that would engender hostility from local residents if acquired is likely to fail the feasibility test.

If a site meets all criteria and is worthy of further consideration, it becomes one member of a *portfolio* of potential sites. For all its worldwide scope and influence, TNC's resources are limited. It cannot acquire every site, and it must make acquisitions that form a *network of reserves* that complement one another in conservation objectives. To aid its decision making process, TNC employs three algorithms for site selection. (1) *The Greedy Richness Algorithm* – Get most species with fewest sites. (2) *The Greedy Rarity Algorithm* – Get the rarest species first, then add increasingly common species after rarest ones are accounted for. (3) *The Connectivity Algorithm* – Provide for landscape scale population resilience by maximizing the likelihood of dispersal among sites by minimizing distances between sites or by providing stepping stone habitats or dispersal corridors between sites. Notice, in this algorithm, how the concepts of percolation theory are implicitly invoked to increase the connectivity of the landscape and the contagion of preserves to one another.

If we employ these algorithms to select the "right" sites for conservation preserves, will we make choices that will be effective in reaching conservation goals? To answer with insight, we must consider further criteria and technological innovation in reserve design. The technology most frequently employed is GAP analysis.

10.6.2. GAP Analysis and Reserve Design

One of the most comprehensive efforts in reserve design and conservation planning is the ongoing Gap Analysis Program, now often referred to simply as GAP or ***GAP analysis***. Originally developed in the early 1990s by J. M. Scott and others at the University of Idaho, GAP uses satellite imagery and GIS technology to make computer-generated regional maps of the distribution of dominant vegetation or geographic distributions of animals species and then relate these distributions to existing conservation reserves (Scott et al. 1993). More specifically, GAP analysis determines, through the use of such computer overlay maps, whether populations of species targeted for conservation fall within the boundaries of currently protected areas (Opdam 2002) and which elements of landscape biodiversity are underrepresented in reserve systems. GAP's sequential tasks are to: (1) map existing vegetation to the level of dominant or co-dominant species (from satellite imagery); (2) map predicted distributions of vertebrate species (using museum and agency collection records with existing general range maps of each species); (3) map public land ownership and private conservation lands; (4) show the current network of conservation lands (the combined distribution of public lands and private conservation lands); (5) compare distributions of native vertebrates and vegetation communities with the network of conservation lands; and (6) from this comparison, provide an objective basis of information for options in managing biological resources. That is, GAP's final outcome is to attempt to identify the "gaps" in the conservation reserve network: where in the landscape do we have significant biodiversity resources that are not protected?

GAP is designed to provide an information base that will enable managers and planners to make the best and most efficient use of land in establishing reserves by showing where conservation efforts should be focused to achieve maximum biodiversity or protection for endangered species. Currently the GAP analysis in the United States, coordinated by the Biological Resources Division of the US Geological Survey, involves 445 contributing organizations and 44 states. With the aid of its GIS applications and technology, GAP can display relationships of interest at varying cartographic scales, distributions of individual species or entire suites of species, and overlay maps of species distributions with different jurisdictions of land ownership and management objectives.

A serious criticism of GAP analysis is that it assumes that all habitat of a specific type will support species that use such habitat, but this is not always the case. Based on theories, models, experiments, and case histories we have examined previously in this chapter, habitat configuration, especially ratios of edge to interior habitat, habitat connections and connectivity, and interspecific interactions are extremely important determinants of habitat use and population persistence in a habitat, but GAP analysis considers none of these things. Further, some have argued that the inventory and monitoring of biotic resources on a national or international scale require a sampling universe composed of broad, landscape-scale assessments. GAP, in contrast, relies mainly on small-scale, low-resolution assessments of biodiversity, and so only infrequently identifies areas that should become candidates for biological protection (Short and Hestbeck 1995). But can we combine the techniques of GAP analysis with an understanding of species-specific habitat suitability models at larger scales?

10.6.3. Reserve Design and Habitat Suitability

To use or not to use. That is the question every species asks when presented with an array of habitat choices, and conservation biologists try to see the world through the eyes of non-human species to anticipate which habitats are worth preserving. Can habitat suitability models be used at larger landscape scales and broader geographic contexts to identify appropriate locations and dimensions of proposed reserves and to evaluate the effectiveness of existing ones in biodiversity conservation? Biologists Carlo Rondinini, Simon Stuart, and Luigi Boitani of the International Union for the Conservation of Nature addressed this problem in an evaluation of conservation planning for African vertebrates (Rondinini et al. 2005). They were able to devise a plan for a systematic reserve selection for 1,223 African mammals and amphibians in which habitat suitability models were used as estimates of the area occupied by each species. A standard conservation goal in reserve design is to conserve 5–10% of present species ranges within the reserve system. Rondinini, Stuart and Boitani wished to determine if, in fact, the present reserve system in Africa really did that for mammals and amphibians. Using data from the IUCN's Global Amphibian Assessment and Global Mammal Assessment, Rondinini et al. determined the geographic range (extent of occurrence) and habitat preferences for each of these 1,223 species. They then used the habitat preference data to construct habitat suitability models inside each species geographic range, and for 181 species, verified the models by comparing suitability levels to presence-absence data collected in the field. They used the suitable areas as estimators of the area of occupancy and compared these to the results of systematic reserve selection based on geographic ranges.

This was an ingenious and inventive use of habitat suitability models in conservation planning and assessment. Unfortunately, the results were discouraging. When Rondinini et al. compared their habitat-based approach to the traditional method of determining refuge placement by overlap with species' geographic ranges, they found that using geographic ranges overestimated the actual area occupied by species and underestimated the total amount of area that needed to be conserved. Further, their analysis revealed that every protected area in Africa contained fewer species than predicted by the analysis of geographic ranges. Because species are more specialized than estimates of geographic distribution suggest, underestimation of land areas needed for reserves is probably not unique to Africa, but a systemic problem in global conservation.

Based on their habitat suitability analysis. Rondinini and his colleagues determined that the reserve system in Africa would need a 30–100% expansion to achieve minimal conservation targets. Existing protected areas cover 3.44 million km^2, or 10% of the African landmass surface. But to achieve the 5% target for geographic ranges, the current reserve system would require an increase of 1.11 million km^2 (32%). The same target would require an increase of 2.36 million km^2 to conserve 5% of suitable ranges and 2.85 million km^2 for highly suitable ranges. Achieving the 10% target for geographic range would take an addition of 1.73 million km^2 to the African reserve system, 2.90 million km^2 to conserve 10% of suitable ranges, and 3.36 million km^2 to conserve 10% of highly suitable areas (Figure 10.17). As the authors themselves note,"This last figure would mean nearly doubling the existing reserve network in Africa" (Rondinini et al. 2005).

This analysis revealed that the present system of reserves in Africa is not sufficient to include even a minimal amount of the range of all mammals and amphibians. It also suggests that planning discussions should be shifted from arguments about the size of the reserve to analysis that more precisely determines the nature of the target. That is, managers should look for the species-specific *quality* of what they are protecting (i.e. the right kind of habitat) instead of the *quantity* of land area in the reserve.

10.6.4. Determining Appropriate Reserve Size

Although habitat quality is an increasing concern in reserve design, the question of how large a reserve should be remains a critical issue in conservation biology. If the purpose of the reserve is to ensure the persistence of a particular species or group of species, then the needs of such species become the operative criteria for reserve size. If time, expertise and money permit, species within the proposed refuge, or at least those of highest priority for conservation, should be subject to a population viability analysis (Chapter 8). Such an analysis can reveal the average minimum viable populations (MVPs) for important refuge species. These MVPs, divided by estimated population densities, should yield the quotient of minimal area for population persistence (Simberloff 1988).

With minimal area estimates in mind, Soulé and Simberloff (1986) offered a three-step approach to the practical problem of estimating the optimal size of a conservation reserve or collection of reserves.The first step is to identify species whose disappearance would significantly decrease the value of the reserve or its diversity, including threatened and endangered species, species of high public visibility or aesthetic appeal, species whose abundance provides an index of habitat quality ("indicator species") and species that create habitat or perform functions that enhance populations of other species ("keystone species"). Second, determine the minimum number of individuals needed to guarantee a high probability of survival for these species. Third, using known densities, estimate the area needed to sustain this minimum population.

The dilemmas of these choices emerge in practical ways when planners can, or must, choose between making the reserve a single large area or several smaller reserves of approximately equal area. Determining the best choice depends upon several factors. First, knowing that smaller reserves will support smaller populations, one must determine the difference between extinction probabilities associated with large and small populations of the most important species. Large differences favor a single large reserve, while small differences argue for several small reserves. A second key question is: how many populations will a series of small refuges preserve, since, presumably, each small reserve will not contain every species that might be present in the single large reserve? Third, what is the correlation in the year-to-year fluctuation of the environments of the populations in the proposed small reserves? If environmental variation is independent (uncorrelated), multiple reserves, even if small, provide a measure of protection against chance environmental disturbances or catastrophes that could reduce or exterminate a single population. On the other hand, if the separate reserves have a high degree of environmental correlation, they confer no such advantage.

If a series of small reserves is considered, what is the probability of recolonization of one of the reserves following a local extinction? If the probability for recolonization is high (individuals disperse well and frequently from patch to patch), there is an advantage to having multiple reserves. But if the probability for recolonization is low, then local extinctions may be more permanent events, and a single large reserve holds the advantage of a larger population less prone to extinction (Simberloff 1988).

Determining reserve size also must consider factors associated with the reserve's habitat heterogeneity and patch dynamics. To preserve both species and habitats, reserves must be larger than the size of the largest disturbance-created patch or "minimum dynamic area", even

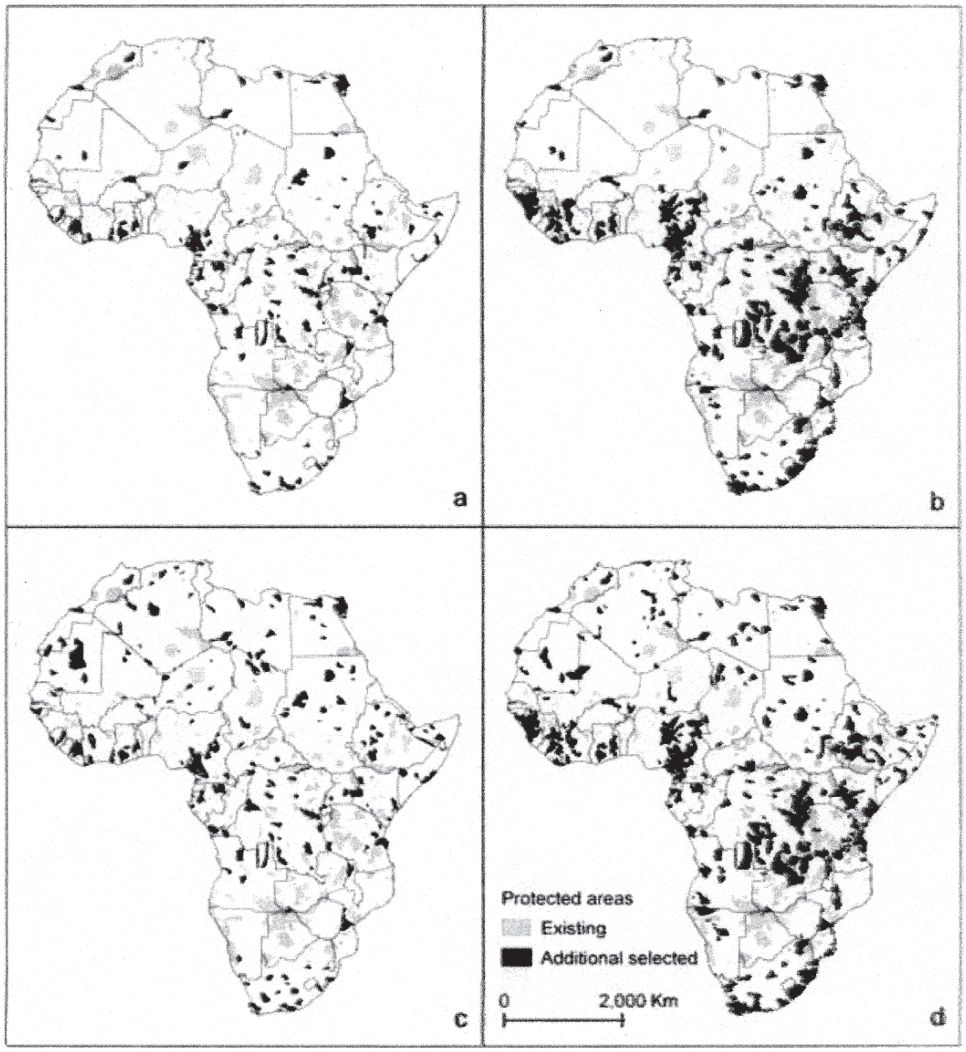

FIGURE 10.17. Location of sites selected under four scenarios of reserve design for African mammals and amphibians. (a) 5% of geographic ranges represented in reserves. (b) 5% of highly suitable habitat areas represented in reserves. (c) 10% of geographic ranges represented in reserves. (d) 10% of highly suitable habitat areas represented in reserves. The fourth scenario (d), although likely the most effective in meeting conservation goals, would require the current African reserve system to be increased by nearly 100%. (Rondinini et al., Habitat suitability models and the shortfall in conservation planning for African vertebrates, *Conservation Biology*, Copyright 2005 by Blackwell Publishing.)

including the rarest kinds of disturbance-created patches, and they should contain separate minimum dynamic areas of each habitat type. Additionally, the reserve should include internal sources for repopulating local extinctions, and should include different ages of disturbance-created patches (Pickett and Thompson 1978).

For all the abstract intricacies that theories of reserve design may generate, conservation biologists must never forget that, in the real world, the most common size for reserves is 10–30 km^2 (Bolton 1997). Regardless of whether or not such reserves are adequate for conserving biodiversity on a theoretical basis, they still represent resources and opportunities for conservation. With intensive and intelligent management, small reserves can make important contributions to conservation efforts.

Even large reserves may not preserve diversity of habitat in a regional landscape, especially if the selection process is insensitive to the realities of patchy habitat distribution. Using a GAP analysis approach, Wright et al. (1994) examined four areas in the state of Idaho, which had been proposed as future national parks (Figure 10.18). Although large, averaging 220,000 ha each, the four proposed areas added little to the number of different vegetation types already under protection, and none met even the modest goal of protecting 10% of the vegetation types in the ecoregion (Wright et al. 1994). Even if areas were expanded, they did little to increase the preservation of habitat and vegetation types. Smaller reserves would have negative effects on population levels of some species, but would not have

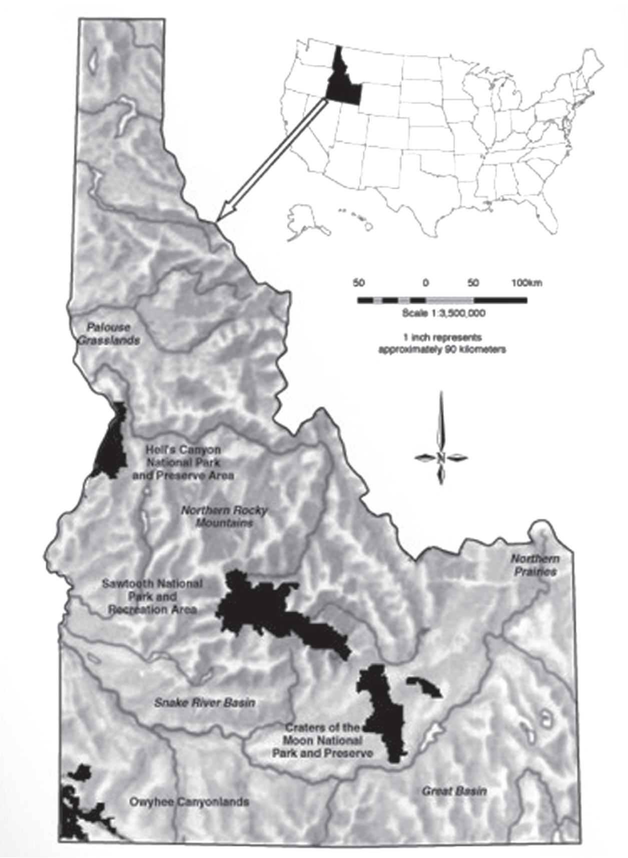

Figure 10.18. Four areas in Idaho proposed for protection as future national parks. Although large, the areas add little to the number of vegetation types under protection and none protect even 10% of the vegetation types in the ecoregion. (Wright et al., An ecological evaluation of proposed new conservation areas in Idaho: evaluating proposed national parks, *Conservation Biology*, Copyright 1994 by Blackwell Publishing.)

reduced the variety of habitats protected. Alternatively, current proposals could have increased the number of habitats preserved with relatively few ha added to their land area. Thus, we see that refuge design, uninformed by ecological data, may have little value in preserving biodiversity.

10.7. Habitat Management on Non-Reserve Lands: Multiple Use and Conservation

10.7.1. Mitigating Human Effects on Non-reserve Lands: The Case of the Line Creek Elk

In a remote region of southeastern Montana, a local population of elk, known as the Line Creek herd, winter in sagebrush-covered foothills on land that is a mosaic of private, state, and federal ownership. The herd's name comes from a stream on their winter range that follows the state line between Montana and Wyoming for several miles. Here the US Forest Service granted a lease for oil exploration to the Phillips Petroleum company. Other state and federal agencies, private conservation organizations, and local residents voiced concern that the drilling activity would displace the elk population and degrade its habitat. There was particular concern that the animals might move permanently south across the state line, depriving the state of Montana of considerable revenue from license and hunting fees.

Phillips agreed to a comprehensive series of rules to minimize the adverse effects of their drilling. The company used the drilling site only in summer and early fall, after elk had moved to other ranges at higher elevations. Access to the site was limited to a single road used only by vehicles of the company and the Forest Service and closed after drilling was completed. Workers were confined to the drill site. After each drilling season, the drilling rig was lowered from a vertical to a horizontal position to make it impossible to see from adjacent drainages, minimizing its visual impact. When drilling activity had ended, the site was re-seeded to native grasses.

The Line Creek elk had been monitored through radio telemetry prior to drilling, and such monitoring was contined during and after the drilling period. Of interest to all, and surprising to many, the population did not move from its original range. The size, shape and position of the herd's home range remained unchanged before, during and after drilling. Elk avoided the drill site itself and increased their use of forested habitats near the well, but did not change their overall patterns of range use, even when such patterns were measured at fine spatial scales (Van Dyke and Klein 1996) (Figure 10.19).

The story of the Line Creek elk is an example of disturbance ***mitigation***. The verb "mitigate" means "to cause to become less harsh or hostile, to make less severe or painful, to alleviate." Although legal protection and environmental policies sometimes provide sufficient authority to end all disturbance that might cause harm to the habitat of an endangered population, non-endangered populations may be no less valuable in their own right, and may be even more important to functioning ecosystems. In managing habitats at regional levels, it is unrealistic to think that all habitat disturbances can be eliminated, but it is not unrealistic to believe that many disturbances can be mitigated.

The Line Creek example provides illustrations of applicable principles of such mitigation. The first is that of ***timing limitations***. If animals use habitats on a seasonal basis, human activities can take place in those habitats in seasons when animals are absent. A second is the principle of ***limited access***. If roads must be built for human activity, their detrimental effects can be reduced if their use and access is

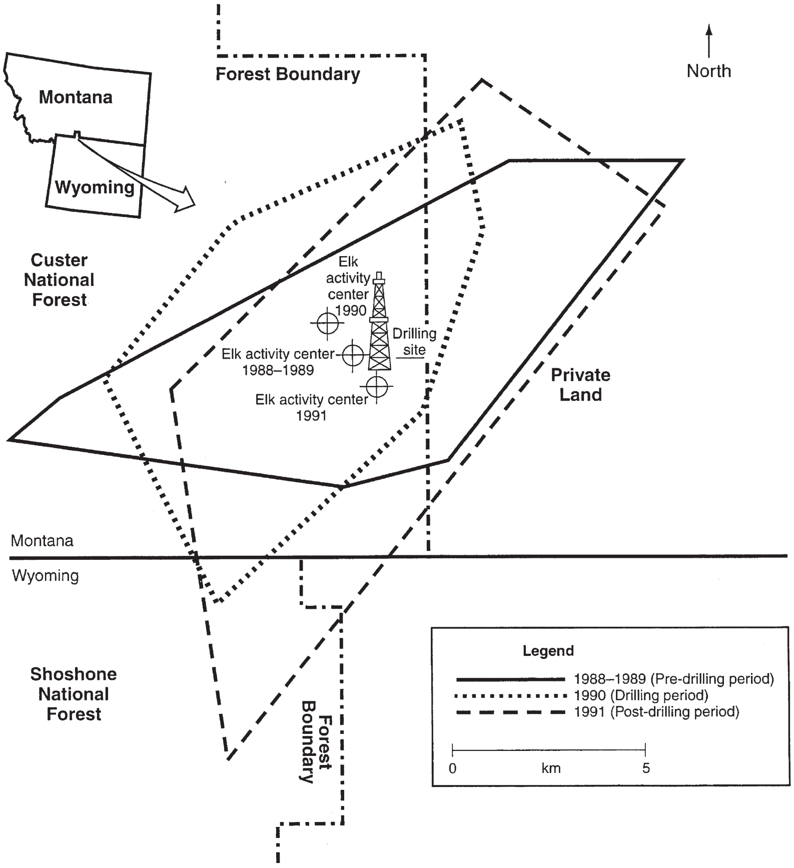

FIGURE 10.19. Seasonal ranges of an elk population before (solid line), during (dotted line), and after (dashed line) oil drilling activity on the population's winter range. Elk avoided the drilling site and altered patterns of habitat use, but, with a variety of mitigation measures in place (see text) did not significantly alter the size or boundaries of their range. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers and Van Dyke and Klein 1996, *Journal of Mammalogy*. Reproduced with permission of the McGraw-Hill Companies, American Society of Mammalogists, and Allen Press, Inc.)

limited to essential activities. A third is the principle of ***visual minimization***, exemplified in the practice of lowering the oil drilling rig to a horizontal position. Reducing the distance at which an object associated with disturbance can be seen by animals reduces the animals' response to the object, and makes more of the area available for the animals' use. A fourth principle is that of ***reclamation***. By immediately reseeding the disturbed site, the oil company began successional activity on the actual drilling site quickly, and acted in a way that could more rapidly return the site to its previously undisturbed state. A fifth principle, although not one apparent in this example, is that of ***no surface occupancy***. Through improving technology like directional drilling, activities such as mining and drilling can increasingly extract resources from beneath a site covered by high quality habitat by surface drilling on a remote site of low quality habitat. This practice can reduce detrimental effects of these activities on sensitive populations.

Although exclusion of human presence may be necessary for some species at all times, and for many species at some times, such exclusion is neither always feasible nor always necessary. Human activities and their disturbances can rarely be eliminated, but they can be managed, and exclusion of human activity is often unnecessary because animals do not use all parts of a landscape. That is why habitat conservation requires an understanding of the habitat preferences of the species to be conserved. Strategies of mitigation can guide conservation biologists to determine ways to permit human use in designated areas with minimal disturbance. In a world where human presence continues to grow, conservation biologists must employ mitigation strategies to maintain viable habitats and healthy landscapes even in the midst of human presence and disturbance.

10.7.2. Managing Non-reserve Lands for Habitat Conservation: The Multiple-Use Module

Site-specific habitat conservation has a long history and admirable record of accomplishment, but also possesses serious weaknesses. Conservation of habitat at individual sites focuses on management at a site-specific level. However, the creation of habitat, as well as the loss of habitat (through disturbance, succession, climate change and human activity) occurs through forces that operate at a landscape level. Unless habitats can be managed and conserved through the same processes that create and destroy them, habitat management and conservation cannot be successful.

One approach that attempts to solve this problem and to integrate the conservation of habitat on managed and reserve lands is the ***multiple-use module*** (MUM) (Harris 1984; Noss and Harris 1986; Noss 1987). First proposed by Harris (1984) for protecting old-growth stands of Douglas fir in managed forests of western Oregon, the MUM system envisions a multiple-use landscape unit ("module") consisting of a fully protected core area surrounded by concentric zones of natural areas used in progressively more intense fashion for recreation and commodity production (Figure 10.20). Individual modules are then connected through landscape corridors to allow movement of animals among modules while allowing for additional uses of resources within the landscape. Buffer zones that surround the core areas of each MUM are intended to: (1) insulate the most sensitive elements in the preserve in a core area free from intensive land use and human disturbance; (2) provide supplementary habitat for animals inhabiting the core area, hence increasing the effective size of the reserve; and (3) provide for a variety of human use and activity in the landscape while minimizing conflicts with other species. The goal is to combine applications of corridors and multiple-use zoning to create an integrated network of clustered reserves (Noss 1987).

Creation and management of an integrated system of MUMs would require applications of ecological restoration, including road closures, reintroduction of extirpated species, removal of human structures and settlements, and restoration of natural disturbances and hydrologic processes (Noss 1987). Although greater human presence and activity would be allowed in buffer zones, their management also would aim at the goals of conserving biodiversity and protecting species of interest (Noss and Harris 1986). Noss and Harris (1986) envision the buffer zones as areas where habitat might be deliberately manipulated to benefit wildlife, but core areas would be considered "inviolate preserves." Proposals for using the MUM concept to integrate conservation landscape planning have been proposed for the north Florida – south Georgia region, for the entire state of Florida (Noss 1987), and for the Ohio Valley in southeastern Ohio (USA) (Noss 1987). But, to date, none of these proposals has been fully implemented.

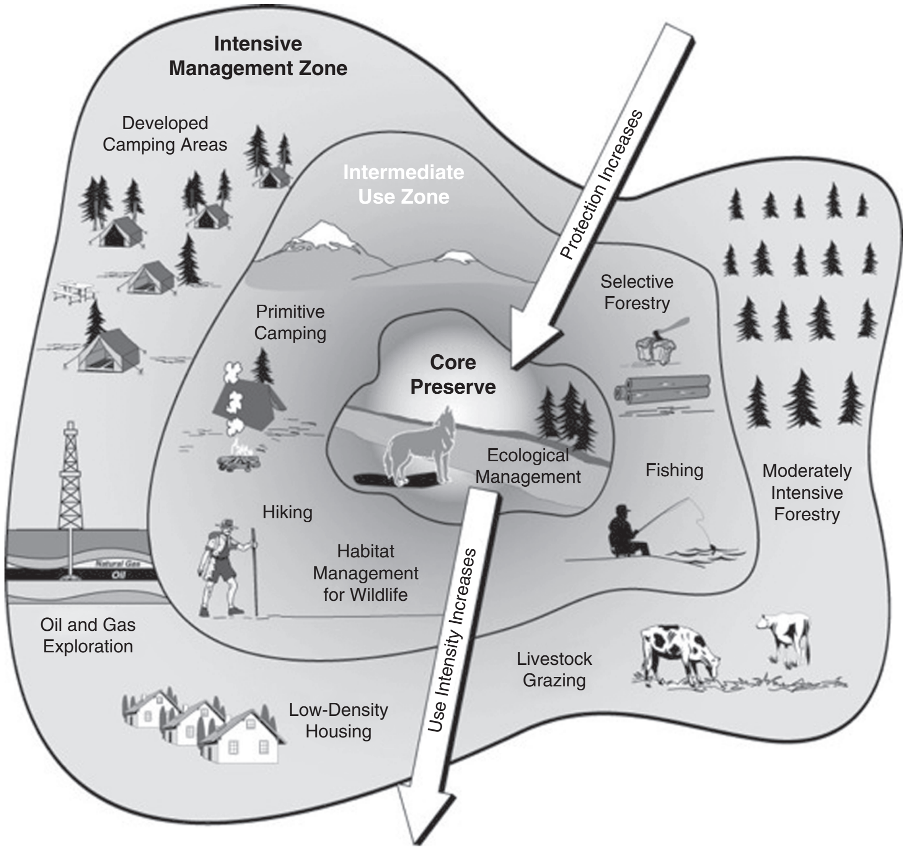

FIGURE 10.20. The multiple-use module (MUM) for habitat and landscape conservation uses a combination of corridors and varying intensities of land use to increase available habitat for species. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

10.8. Synthesis

Habitat conservation is the foundation of population conservation. Yet conservation biologists still struggle to understand the separate and interactive effects of habitat loss, habitat fragmentation, and habitat isolation on plant and animal populations, to communicate these effects coherently to the public, and to translate their understanding into meaningful policies that effectively manage habitat and the processes that shape it. The importance of habitat is recognized in concepts like that of "critical habitat," written into the US Endangered Species Act (Chapter 3), yet often ignored in many other conservation laws. Likewise, most conservation organizations present their mission in terms of species, not landscapes. A notable exception, The Nature Conservancy, offers an example of how to articulate an alternative conservation vision. TNC states that its mission is "to preserve the plants, animals, and natural communities that represent the diversity of life on Earth by protecting the lands and waters they need to survive," a complement to its memorable organizational slogan, "Saving the last great places."

More conservation organizations must come to The Nature Conservancy's level of awareness of the importance of habitat conservation. Perhaps humans have been reticent to embrace habitat conservation as enthusiastically as species conservation because habitat conservation is fundamentally an issue of *land use*. Habitats cannot be conserved in zoos. They persist only if people choose to occupy less land, and to use the land they occupy in less destructive ways. This dilemma is what Aldo Leopold called "… the oldest task in human history: to live on a piece of land without spoiling it" (quoted in Freyfogle 2003:141). Habitat conservation is a commitment to pervasive changes in practices of human residence and land use. Humans must determine what critical habitat components are, and then find ways to use landscapes in ways such that their presence does not destroy these components, but preserves them, at least in part, in place and function. If refuge design is not complemented by the presence of sufficient functional habitats in the surrounding and vastly greater array of non-reserve lands, no population, especially of large, mobile species, has real hope of long-term persistence.

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11

The Conservation of Aquatic Systems

> *…a river is more than an amenity. It is a treasure. It offers a necessity of life that must be rationed among those who have power over it.*
>
> Oliver Wendell Holmes, 1931

In this chapter, you will learn about:

1. **The ecological properties of aquatic habitats**
2. **Types of freshwater and marine ecosystems**
3. **Conservation problems, goals, and management strategies associated with freshwater and marine ecosystems**

11.1. Conservation Challenges of Aquatic Habitats

11.1.1. Overcoming the Terrestrial Bias

The majority of literature in conservation biology, as in the rest of biology, focuses on terrestrial environments and the creatures that inhabit them. Yet 71% of the globe is covered by oceans, not land. Freshwater and marine environments may hold the majority of all earth's species, but because they are foreign and threatening to us as humans, and more difficult to investigate, they are not as well studied as terrestrial sites. The resources of aquatic habitats are vast and essential, but even those we use most frequently are mysterious to us. We often receive them, or exploit them, without truly understanding their value or the processes that sustain them.

Aquatic creatures are important in the diet of most people throughout the world, yet we have no real idea of the sizes of the populations that support these fisheries, especially in the oceans. Our lakes, rivers, and seas are repositories for all types and quantities of human and industrial refuse, yet we do not know the capacity of these systems to hold such waste, or its effects on ecosystem functions. The majority of our commercial fisheries are fully exploited, over-exploited, or in decline, yet we go on taking. The oceans of the world have long been one of the principal regulators of its climate, yet, as human activity alters such climate, we are only beginning to appreciate how such changes will affect ocean systems. Subsurface ocean topography and structure determine the abundance of many creatures on which humans depend for food, yet humans alter ocean topography and structure in harvesting food and other resources. Such alterations leave us with less food to harvest and fewer resources to use. Because aquatic habitats are different from terrestrial ones, the problems associated with their conservation also are different. Their uniqueness deserves special attention.

11.1.2. Conservation Challenges of Freshwater Habitats

Freshwater habitat quality is degraded worldwide by a small constellation of common factors and processes. The most important threats to freshwater streams and lakes are physical habitat alteration, chemical alteration or pollution of the water, introduction of exotic species (Abell et al. 2000), and, in streams and rivers, alteration of flow regimes. Alteration of flow rates and habitat structure, pollutants, and exotic species have rendered many rivers unfit for most human uses. A recent survey of some 643,000 miles of US waterways found that only 56% could support multiple uses such as drinking water, fish and wildlife habitat, recreation, and agriculture (Abell et al. 2000). In the 44% of rivers that could not support multiple use, the most important problems were chemical alternation or pollution of the water, specifically sedimentation, nutrient overloading, also known as eutrophication, and acidification. We have explored population traits and patterns of spread characteristic of invasive species (Chapter 9). Here we examine briefly two other factors that are unique problems in aquatic habitats.

Invasive species, although threatening all types of native populations worldwide, are a significantly greater problem in aquatic habitats than in terrestrial ones. In Canada for example, invasive species are a primary threat to 26 out of 41 listed fish species, and 6 of 11 listed mollusk species (Dextrase and Mandrak 2006). Disturbed aquatic systems, and particularly those associated with urban areas or other regions of high human population densities and use, are more vulnerable to invasions than undisturbed systems, partially because they lack the resiliency of undisturbed systems and partly because their exposure to increased levels of human use lead to greater and more frequent introductions of non-indigenous species, accidentally or on purpose, by humans (Dudgeon et al. 2006). Many invasive aquatic plant species, particularly in wetlands, tend to be large or spreading invasive perennials, such as purple loosestrife, reed canary grass (*Phalaris arundinacea*), alder buckthorn (*Rhamnus frangula*), and European frog-bit (*Hydrocharis morsus-ranae*), which can, under the right (or should we say "wrong") conditions, become dominants in freshwater lakes, streams, and wetlands. Interestingly, although the presence of such species tends to depress biodiversity, mainly through the suppression and eventual loss of rare species, such presence has no more depressing effect than that of native dominant wetland species such as cattail (*Typha* spp.), meadow willow (*Salix petiolaris*), or yellow pond lily (*Nuphar variegatum*) (Houlahan and Findlay 2004). Thus, again, the tendency of human disturbance to reduce, intentionally or unintentionally, the biodiversity of natural aquatic and wetland plant communities tends to increase the probability that, once disturbed, invasive dominants can become established and reduce native biodiversity even further.

Eutrophication occurs when nutrients, particularly nitrogen and phosphorus, are released to rivers from upstream or surrounding agricultural areas (in the form of fertilizer runoff) or from towns and cities (in the form of human waste) (Brönmark and Hansson 1998). Higher levels of nitrogen and phosphorus trigger a chain of events that begins with a massive increase in the growth of primary producers (usually limited by a scarcity of these nutrients in freshwaters). Periphytic (attached) algae and submersed macrophytes increase in biomass at the beginning of the process, but then decline as phytoplankton and cyanobacteria ("blue-green algae") increase in abundance and reduce the amount of light that filters through the water. Dead organisms accumulate as sediment and bacteria that remove minerals from decaying organic matter consume large amounts of oxygen, which they extract from the water. Fish kills of some species follow as oxygen is depleted, but cyprinid fishes (Family Cyprinidae, carps and minnows) increase because they can survive in poorly oxygenated waters and are efficient predators of zooplankton, whose numbers increase in the initial stages of eutrophication. As a result of cyprinid predation, grazing zooplankton decrease. Levels of phytoplankton, the prey of zooplankton, then increase, further increasing turbidity (Brönmark and Hansson 1998). As eutrophication progresses, the biological community is altered, and the lake declines in value as a source of drinking water, recreation, and food.

Acidification is a process through which the pH of surface freshwaters, especially lakes, declines (becomes more acidic) because of inputs of acidic precipitation in the form of rain, snow, or fog. Emissions of hydrogen sulfide (H_2S), produced by the burning of coal to generate electricity, and nitrous oxide (NO), a typical exhaust waste from cars, can combine with atmospheric water vapor to form weak concentrations of sulfuric acid and nitric acid that fall as precipitation into the stream or its surrounding drainage area.

Acidic inputs generally do not affect pH in areas where soil and rock substrates contain significant amounts of calcium carbonate ($CaCO_3$) or other carbonate compounds. These compounds react with water to form carbonate and bicarbonate ions that can buffer a system against acidic inputs. In areas without such buffering capacities, however such as those with granitic substrates or granitic-derived soils, the same inputs of acid precipitation can have disastrous effects on aquatic communities.

The sequence of events begins with a lowering of pH in the aquatic system due to acidic inputs, especially during periods of heavy rain or during spring snowmelt. The most common and immediate effect of lower pH is a reduction or cessation of reproductive effort in many species of fish, amphibians, and aquatic invertebrates, and some species may suffer direct mortality. An indirect but often more devastating effect of the lower pH is a change in the chemical reactions occurring in the aquatic system, especially in metallic ions such as aluminum, lead, or cadmium. Aluminum is especially deadly to fish because, under acidic conditions, it binds to their gills and impedes respiration (Brönmark and Hansson 1998). When fish populations are reduced in acidified lakes, many invertebrates are released from predation pressure and invertebrate populations may then grow (especially predatory invertebrates) (Brönmark and Hansson 1998). In addition, once aluminum begins to precipitate out of solution, it binds with phosphorus, causing both to precipitate out as aluminum phosphate. Such a reaction takes phosphorous out of the system and makes it unavailable as a nutrient for organisms.

11.2. Management of Freshwater Habitats for Conservation

11.2.1. Managing Chemical and Physical Inputs to Aquatic Systems

Preserving and restoring the conservation value of aquatic systems can be accomplished only by active management. In North America, the leading threats to freshwater fauna are increased sediment loads and nutrient inputs from agriculture, interference from exotic species, altered hydrologic regimes associated with dams, and acidification. In particular, problems such as sedimentation, eutrophication, and acidification are *input-oriented* problems, and their best solution lies in input regulation.

The sources of sedimentation and eutrophication are soil and fertilizer inputs, respectively, from surrounding lands, especially agricultural lands, and urban waste. Both are usually non-point source pollution problems, aggravated through high levels of erosion from surrounding agricultural lands. Thus, the best management to address both problems would be socio-political in nature, specifically through laws and policies that (1) reduced the use of fertilizers, particularly on highly erodible lands and on lands near watersheds; (2) required removal of fertilizers, especially phosphorus, nitrate, and nitrite from urban sources before allowing urban discharge to proceed downstream; and (3) reduced erosion on agricultural lands through increased vegetative cover bordering streams and through cultivation methods less destructive of soil structure. However, managers of specific aquatic systems, such as individual lakes and streams, lack power and jurisdiction to implement such sweeping changes over entire regions and drainage basins. The systems they are to conserve are degraded by inputs from surrounding land-use practices that they cannot directly control. In such cases, managers must use site-specific approaches within their jurisdiction. They must stop such inputs from entering the system as they reach it, or they must remove or neutralize such inputs.

The most direct ways to stop such inputs into an aquatic system are (1) to install filters and other devices at the proximate source of input, such as the inflow stream, that remove the sediment and fertilizer when it arrives and (2) surround shorelines and banks with vegetation that can achieve high levels of phosphorus and nitrate/nitrite uptake from runoff. However, the installation of filters and other devices is expensive, and the planting and management of appropriate vegetation both costly and labor-intensive.

Such practices may dramatically lower the amount of sediment and fertilizer entering an aquatic habitat, but reductions of fertilizer input will not necessarily restore the damage done by previous nutrient loading. What does one do with the phosphorus and other nutrients that have already entered, and now remain in, the system? Remedies for this problem are dredging, chemical manipulation, and biomanipulation.

Dredging is the most direct approach. In this method, sediment from a eutrophied lake, pond, or wetland is physically scraped off the bottom using large, earth moving machines. Such sediment may then be placed in a different, artificially constructed basin where the phosphorus is removed by physical or chemical means. Thus purified, the sediment may then be returned to the system. While admirably direct, dredging is expensive, labor intensive, and disruptive to existing populations and communities, especially the benthos. Dredging may require temporarily draining the system, and the method is seldom suitable or effective in large, deep lakes. During the dredging operation itself, the aquatic habitat may not be suitable for other uses by humans.

Some chemical methods can be effective in removing phosphorus by converting it into other chemical states or that prevent it from entering or interacting in the system. One of these is the so-called Riplox method (Brönmark and Hansson 1998). In this approach, the sediment surface is first oxidized, causing the phosphorus in it to precipitate in metal complexes. Then calcium nitrate ($Ca(NO_3)_2$) and iron chloride ($FeCl_3$) are added, increasing levels of oxygen and iron concentrations present. The pH of the system, which would tend to decline at this point, is stabilized through the addition of calcium hydroxide ($Ca(OH)_2$). At a suitable pH, denitrifying bacteria in the sediment will transfer nitrate in the added calcium nitrate to nitrogen gas (N_2), releasing it to the atmosphere. If these reactions proceed, a chemical "lid" is placed over the surface of the sediment that prevents the release of phosphorus from the sediment into the water.

The third method, biomanipulation, attacks the eutrophication problem by manipulating populations of living creatures in the system. First, the densities of zooplanktivorous fish (generally the cyprinids) are reduced, either by adding piscivorous (fish-eating) species or by extracting the cyprinids directly by trawling with gill nets. Theoretically, if the number of zooplanktivorous fish are reduced, zooplankton populations will grow and the grazing rate on algae and phytoplankton will increase. As a result, algal blooms will decrease and water clarity will improve. Biomanipulation has worked best where at least 80% of the zooplanktivorous fish are removed, and its success appears not to be due to the reasons originally believed. Rather, removal of the fish seems to lead to an increase in the levels of submerged macrophytic plants and periphytic algae at the sediment surface. These in turn absorb large amounts of nutrients that are then no longer available for phytoplankton and oxidize the surface of the sediment, reducing the absorption of phosphorus into the water. Removal of fish reduces bottom disturbance by benthic-feeding fish, reduces excretion of nutrients by fish, and reduces phosphorus released into the water from the bodies of fish when they die and decompose.

Interestingly, lake systems can, with respect to phosphorus, exist in so-called ***alternative stable states***, in which, at similar nutrient levels, they may be dominated by submerged macrophytes in clear water or by high densities of phytoplankton and associated turbid water (Genkai-Kato and Carpenter 2005). The transition from one state to the other is not gradual but rapid. The theory can be illustrated visually by the "marble in a cup model" (Scheffer 1990) (Figure 11.1). Under high levels of nutrient enrichment, the lake can exist only in a turbid state. As phosphate levels decline, alternate stable states are possible, depending on which way the system (marble) is pushed. If, for example, macrophytes and periphytic algae can be well established at intermediate nutrient levels, they can take in excess amounts of phosphorus ("luxury uptake") that limits availability of phosphorus for phytoplankton and prevents their populations from increasing (and prevents the clarity of the water from decreasing). The lower the level of nutrients in the water, the more stable the clear state becomes. If the model has represented the system correctly, it demonstrates that the system's condition is a function not only of nutrient inputs and fish populations, but also of populations of macrophytes and periphytic algae. Further, the system's future state is dependent on its present state, especially on how well established populations of macrophytes and algae are and how much phosphorus they can absorb. Although this model is theoretical, it has empirical support from

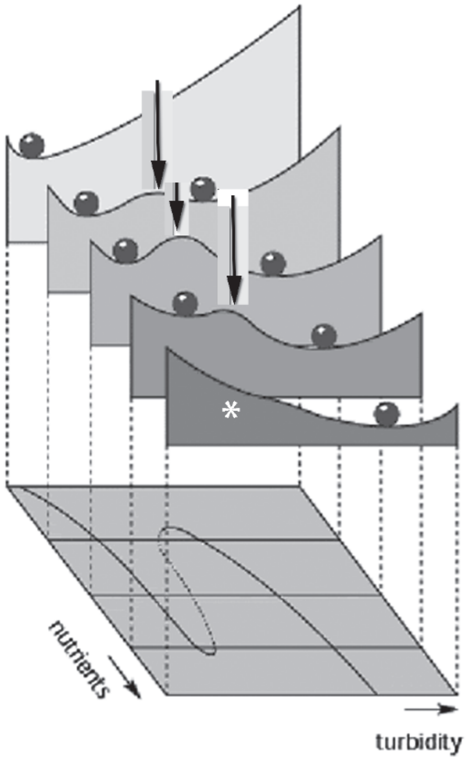


FIGURE 11.1. The "marble in a cup" model of alternative stable states of lakes relative to different levels of phosphorus inputs. Stability of the system is achieved through a combination of biomanipulation and control of phosphorus inputs, but not one or the other exclusively. Typically, turbidity increases as nutrient levels increase. At low nutrient level increases, turbidity may not change unless a disturbance (represented by arrows) occurs. However, at a certain point (∗) nutrient levels are too high for the water to remain in a clear state. (Scheffer 1990. Copyright 1990 Springer-Verlag, New York, Inc. With the kind permission of Springer Science and Business Media.)

studies of Swedish lakes that exhibit alternative stable states (Blindow et al. 1997).

Motomi Genkai-Kato and Stephen Carpenter of the University of Wisconsin's (USA) Center for Limnology took the concept of alternative stable states a step further through the development of a complex mathematical model designed to predict lake transformations, and the relative possibilities of restoring eutrophied lakes if a transformation occurred. Using empirical data from their own and other studies of lake eutrophication, Genkai-Kato and Carpenter found that both biotic and abiotic variables, and their interaction, strongly affected not only the stable state of a lake, but also its potential for restoration. Shallow lakes could be protected, in part, from eutrophication by the presence of macrophytes that removed phosphorus from the water (Figure 11.2A). Deep lakes could be protected, in part, through the dilution of phosphorus concentrations in their deepest layers (hypolimnion). The model predicted that lakes most vulnerable to eutrophication, and least restorable after eutrophication, would be lakes of intermediate depth. Intermediate depth lakes were too deep to receive the benefit of phosphorus uptake by macrophytes and too shallow to sufficiently dilute phosphorus in deeper waters. Regardless of depth, eutrophication was more likely to occur, and harder to reverse, at warmer temperatures (Figure 11.2B). In fact, the model predicted that, in warmer lakes, shifts to alternate states (for example, clear to turpid) would occur at lower levels of phosphorus input and the effects of the shift would be larger (Genkai-Kato and Carpenter 2005). This finding is disturbing in light of the pattern of global climate warming the Earth is now experiencing (Chapter 5), and the fact that it is very difficult for managers to regulate lake water temperature through any conventional management strategy.

11.2.2. Managing Freshwater Systems Through Riparian Zones

Riparian vegetation refers to plant communities adjacent to a body of water, such as a lake or stream. Riparian zones, aside from their potential importance as corridors that link populations in different areas, profoundly affect the quality of freshwater ecosystems because they can modify, dilute or concentrate substances from terrestrial environments in the drainage basin before they enter the drainage basin. Thus, riparian zones are the link between an aquatic system and its terrestrial context. Riparian zones as narrow as 10–30 m in width can moderate temperatures, stabilize banks and provide essential material inputs to biotic communities. Riparian vegetation of similar widths (9–45 m) can substantially reduce inputs of sediments from the surrounding landscape (Osborne and Kovacic 1993). Finally, riparian vegetation, deliberately arranged as buffer strips along streams, lakes, or wetlands, can reduce inputs of nutrients such as phosphorous and nitrogen from a surrounding and heavily fertilized agricultural landscape.

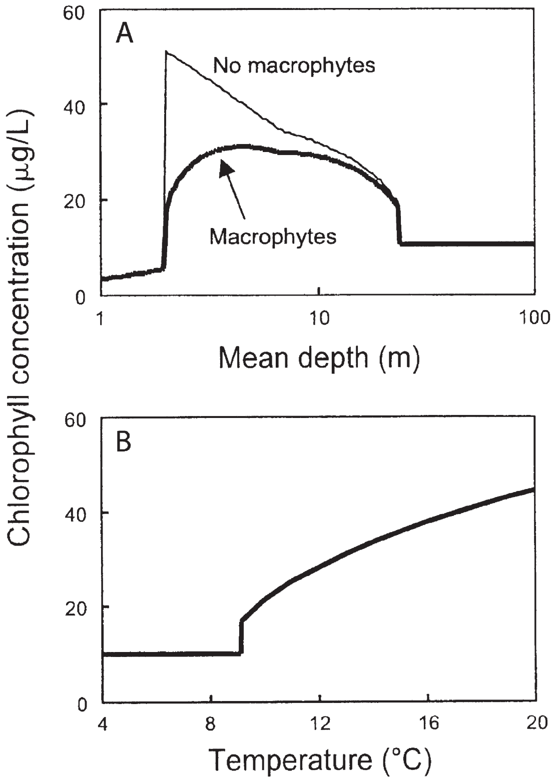


FIGURE 11.2. (A) The presence of aquatic macrophytes, rooted in the littoral (shoreline) zone of a lake, can reduce concentrations of chlorophyll, an index of eutrophication, in water depths of 2–10 m. At greater depths, there is insufficient light to establish substantial populations of macrophytes, with consequent minimal effect on chlorophyll concentrations in the water. (B) As water temperature warms, chlorophyll concentrations increase rapidly, making eutrophication in the lake more likely to occur and less likely to be reversible by any management actions. (Genkai-Kato and Carpenter 2005. Eutrophication due to phosphorus recycling in relation to lake morphometry, temperature, and macrophytes, *Ecology* 86:210–219, Reprinted by permission of the Ecological Society of America.)

The quality of riparian vegetation is often especially critical to egg, larval, fry, and juvenile stages of fish which have more narrow environmental tolerances than adults. For example, removal of riparian vegetation in the South Umpqua River of Oregon has been a contributing factor to declines in this river's Chinook Salmon (*Oncorhynchus tshawytscha*) population. Such removal, primarily due to logging and road construction, has contributed to increased erosion and subsequent siltation that covers gravel substrates needed for egg-laying habitat, with associated decreases in oxygen concentration and light penetration. Such removals increase evaporation in the stream, leading to reduced summer stream flows. In spring, the removal of riparian vegetation increases runoff during peak flows, washing out deposits of gravel and debris from streambeds that are essential elements of salmon habitat. The most serious effect is that, without riparian vegetation, summer water temperatures in some sections of the South Umpqua have risen above lethal levels for salmon (26°C) in recent years (Ratner et al. 1997). Ratner et al., who conducted a population viability analysis on this population of salmon, noted that "if habitat degeneration continues as the historical rate … the population has a 100% probability of going extinct within 100 years" (Ratner et al. 1997). Ratner and her colleagues advocated closing roads along the river and its tributary streams and beginning a process of active riparian vegetation restoration as essential steps to maintain this population.

Recent research also reveals that riparian zones, specifically the preservation of riparian vegetation, may be the key management action in protecting the biodiversity of freshwater streams from degradation caused by increasing human populations around them. Urbanization can not only degrade streams through direct effects of increased sedimentation and pollution, but also by restricting species dispersal within and among stream reaches. Just as terrestrial habitats can best be understood as occurring in patches (Chapter 10), so can stream habitat. In a landscape fragmented by urbanization, streams are isolated from one another by interposing urban "nonhabitat" that stream-dependent species cannot cross. This isolation can occur because most stream invertebrates live as larvae in the stream but live out of the stream as adults, and may disperse as adults from one stream to another before they breed, eventually producing larvae in a different stream. The resulting fragmentation can make it impossible for stream-dependent invertebrate species to move across a landscape to a new stream. Thus, urbanization can not only alter instream habitat, chemistry, and flow regime, but also fragment terrestrial habitat necessary for dispersal of stream invertebrates.

To evaluate the severity of this problem and its effect on stream-dependent invertebrate communities, Mark Urban and his colleague's studied invertebrate communities in streams experiencing different levels of human and urban influence in the West, Mill, and Quinnipiac Rivers near New Haven, Connecticut (USA) (Urban et al. 2006). They considered three hypotheses to explain invertebrate biodiversity in streams. (1) Invertebrate community structure is best predicted by local instream habitat and physiochemical conditions. (2) Coarse-scale changes in watershed land use and riparian vegetation best predict invertebrate community structure. (3) Fragmentation and isolation among stream reaches best predicts variation among invertebrate communities by limiting and reducing dispersal among adult invertebrates (Urban et al. 2006).

Overall, Urban et al. found a strong negative relationship between stream invertebrate biodiversity and urbanization (Figure 11.3). In contrast, a stream's local habitat conditions, including such things as substrate, discharge, water chemistry, and physical instream features, were poor predictors of stream invertebrate community composition and abundance. Thus, invertebrate community structure was not well explained by variation in local stream habitat and physiochemical condition (microhabitat) and the first hypothesis was not supported. Rather, stronger predictors of stream invertebrate composition and abundance were variables associated with riparian vegetation, specifically, the level of forest stand diversity and vegetation density along a stream, the characteristics of natural vegetation within the watershed, especially the percentage of forest remaining within the watershed (second hypothesis), and the proximity of adjacent streams to one another (integrity of the stream "network," third hypothesis). The greater the amount of riparian vegetation, forested landscape in the watershed, and proximity of streams in a drainage network to one another, the greater the level of invertebrate biodiversity in any given stream (Figure 11.4).

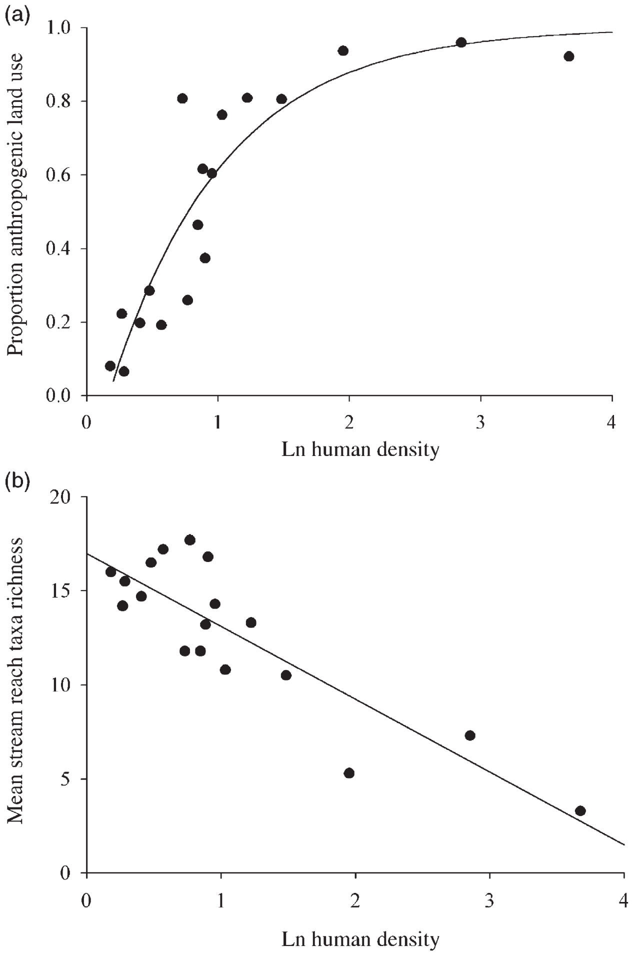


FIGURE 11.3. Relationships among stream invertebrate biodiversity, watershed land cover, and household density in a watershed in Connecticut, USA. (a) Proportion of watershed area devoted to anthropogenic land uses as a function of household density. Model fit by nonlinear regression (N = 18; model: y = 1–1,21 exo$^{-1.15x}$; $P < 0.01$. (b) Mean stream reach (section) taxa richness versus human household density. Model fit by OLS regression ($N = 18$, $R^2 = 0.75$, $P < 0.0001$). (Urban et al., Stream communities across a rural-urban gradient, *Diversity and Distributions*, Copyright 2006 by Blackwell Publishing. Reprinted with permission of Blackwell Publishing and M. C. Urban.)

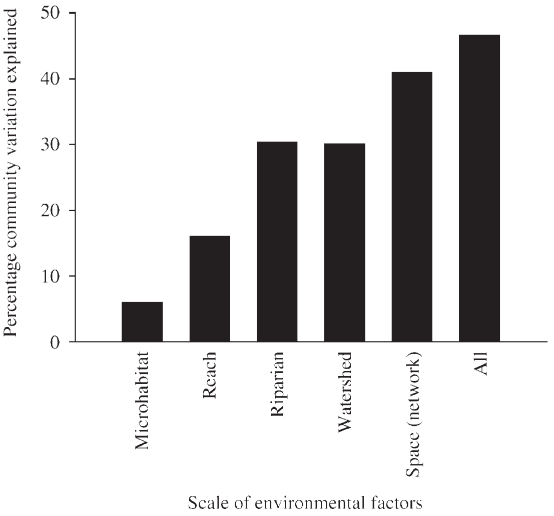


Figure 11.4. Percentage of variation in stream invertebrate community composition and abundance explained by microhabitat, stream reach (section) characteristics, amount of riparian vegetation, proportion of remnant (original) vegetation in watershed, and average distance of adjacent streams to one another. (Urban et al., Stream communities across a rural-urban gradient, *Diversity and Distributions*, Copyright 2006 by Blackwell Publishing. Reprinted with permission of Blackwell Publishing and M. C. Urban.)

In these streams experiencing an increasing intensification of urbanization, Urban et al. demonstrated that it was the amount of remnant natural vegetation along riparian corridors and within watersheds that were two of the most important predictors of invertebrate communities. But increasing urbanization does not necessarily require loss of riparian vegetation, such as reduced forest tree species diversity or tree density along a stream. Such vegetation can be intentionally spared during the development process. If development planners identify these attributes as variables to conserve during the development, they may be able to conserve high levels of stream invertebrate biodiversity despite an increasing level of urbanization in the larger landscape.

11.2.3. Organizing Information About Freshwater Ecosystems for Conservation – The Problem of Classification and Prioritization

11.2.3.1. Coarse-Filter Approaches for Regional Representation – The Nature Conservancy's Nested Classification System of Aquatic Habitats

In areas of the world where species data are deficient, regional habitat representation, a specific form of the more general "coarse-filter" approach to biodiversity conservation, serves as the primary tool for representing biodiversity in regional conservation planning. The Nature Conservancy, administering the largest system of private terrestrial refuges in the world, is also involved in the global conservation of freshwater aquatic ecosystems. As a first step toward organizing information about such systems worldwide, TNC has developed a coarse-filter classification system (Chapter 4) for streams, lakes, and rivers using four spatial levels (Figure 11.5).

The highest level in the classification is called the ***aquatic zoogeographic unit*** (AZU), and serves as the overall planning unit in initial conservation assessment. AZUs conform to major freshwater drainage boundaries, generally 10,000–100,000 km^2. They are distinguished by differences in continental and regional zoogeography, which result from differences in initial zoogeographic sources, patterns of drainage connections, and biotic changes over time in response to climatic and geologic events. AZU planning units delineate the area to be classified for a particular project, and are differentiated on the basis of large-scale ecological differences rather than geopolitical boundaries.

The second level of the analysis relies upon identification of ***ecological drainage units*** (EDUs) within an AZU. EDUs represent regional biodiversity distinctions within AZUs, and are generally 1,000–10,000 km^2 in size. EDUs are delineated and classified by identifying areas with similar biotic patterns and represent a finer scale of physiographic and zoogeographic diversity, allowing the selection of rivers and lakes for conservation to be stratified by environmental and biological differences within an AZU.

The third level of classification are the ***aquatic ecological systems*** (AES) residing within a particular EDU. AESs are stream networks representing a range of areas with distinct geomorphological patterns tied together by similar environmental processes such as hydrologic, nutrient, and temperature regimes. Patterns of environmental conditions that determine the characteristics of freshwater ecosystems and influence biotic patterns are used to classify the AESs. Freshwater ecosystem attributes such as water-body size, hydrologic and temperature regime, chemistry, drainage network position, local connectivity, elevation, and gradient can result in distinct aquatic assemblages and population dynamics between and within streams and lakes. Thus, it is an individual AES that can become the actual conservation target if it contains high levels of regional biodiversity, and if resources and circumstances permit the preservation of the entire unit.

The fourth level of TNC's classification system is the *macrohabitat*, representing finer scale classification units that can be used to create the AES. Some parts of the world do not have sufficiently detailed information on aquatic systems to identify individual macrohabitats within AESs, and, if so, this classification can be omitted and targets for conservation reserves designated by selecting appropriate AES units. Where sufficient information exists to permit identification of macrohabitats within an

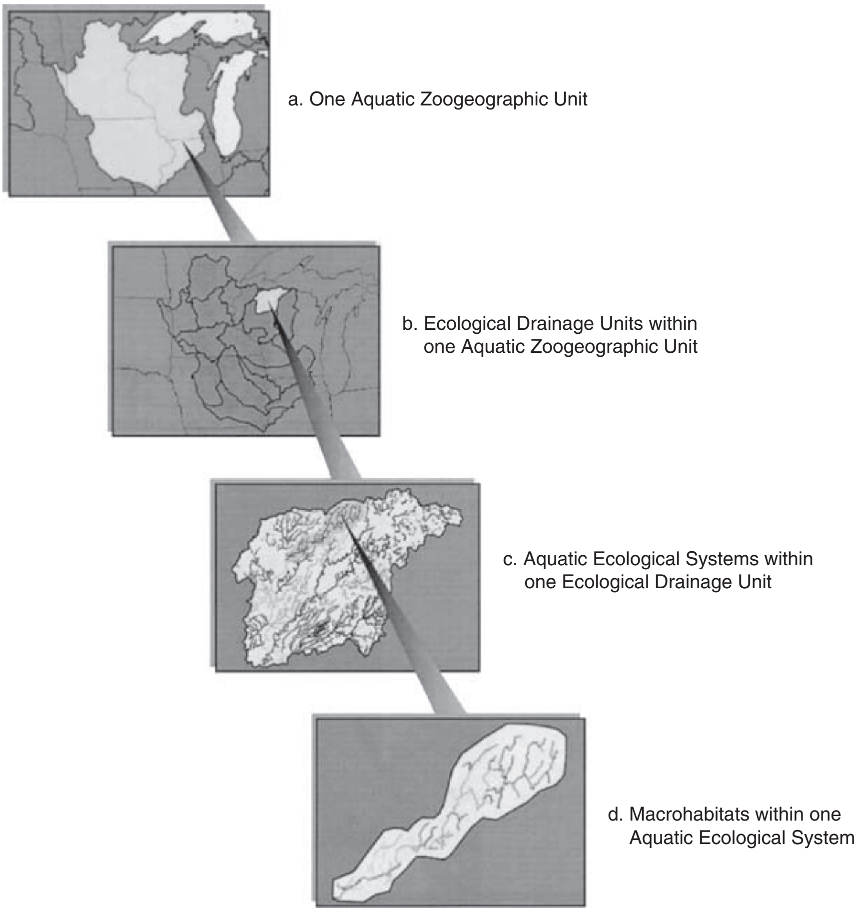


FIGURE 11.5. A four-tiered, hierarchical framework for classification of freshwater systems for conservation developed by The Nature Conservancy (TNC). The highest level is (a) that of aquatic zoogeographic units (AZUs) (approximate scale 1:26,000,000). (b) Ecological drainage units (EDUs) are nested within AZUs (approximate scale 1:26,000,000). (c) Aquatic ecological systems (AESs) are nested within EDUs (approximate scale 1:4,000,000). (d) Macrohabitats are nested within AESs (approximate scale 1:1,200,000). (From *Drafting a Conservation Blueprint: a Practitioner's Guide to Regional Planning for Biodiversity* by C. R. Groves. Copyright 2003 by Island Press. Reproduced by permission of Island Press, Washington, DC, and Jonathan V. Higgins.)

AES, these can serve as conservation targets at smaller scales. The last two levels consider how the physical environment shapes local distribution patterns of aquatic organisms and thus are described using only abiotic variables (Higgins et al. 2005).

TNC uses these four levels because there are spatial data available, mainly via remotely sensed data interpretable via GIS, to classify and map ecological patterns at scales that are known to shape freshwater biodiversity patterns. Such a classification scheme can operate using either "top-down" or "bottom-up" approaches. In regions where fine-scale, high-quality hydrogeographic data and digital versions of other relevant data layers are available, TNC has developed an automated, unsupervised, bottom-up classification approach that can be conducted to map AES. In this approach, the classification is implemented by mapping relevant classification attributes onto the stream arcs and lake polygons in the hydrographic data of a GIS file with a set of automated GIS decision-criteria algorithms created specifically for this purpose. In contrast, a top-down classification is used in areas where GIS data are insufficient for identifying stream characteristics at the level of individual habitats. In these situations, the macrohabitat classification is omitted, but AESs are defined based on similar environmental attributes (Figure 11.6) (Higgins et al. 2005). Regardless of which strategy is used, this approach provides TNC with a rapid and pragmatic way to organize information on freshwater ecosystems at scales appropriate for ecoregional assessment.

Jonathan Higgins and his colleagues at The Nature Conservancy, who helped to develop this classification system, note that "Without the coarse-filter targets provided by the classification, the known location of rare and endangered species would drive most conservation priorities, which would likely exclude numerous species and ecosystems representative of the ecoregion. This is especially important in regions that lack rare and endangered or endemic species" (Higgins et al. 2005:441–442).

By themselves, these classification units will not predict biotic composition. Rather, the rationale supporting the classification's use is that it will allow conservation planners to develop plans that more efficiently identify areas within a planning region that comprehensively capture common

FIGURE 11.6. Example of a top-down classification from a portion of the Alto Cuiabá ecological drainage unit in the upper Paraguay River Basin, an approach used in areas where GIS data are insufficient for identifying stream characteristics at the level of individual habitats. In these situations, the macrohabitat classification is omitted, but AESs, such as those shown in this drainage unit, are defined based on similar environmental attributes. Here examples of different AES types are represented as stream networks. (From *Drafting a Conservation Blueprint: a Practitioner's Guide to Regional Planning for Biodiversity* by C. R. Groves. Copyright 2003 by Island Press. Reproduced by permission of Island Press, Washington, DC, and Jonathan V. Higgins.)

and representative biota across environmental gradients than do plans that do not use such coarse-filter targets. Although this approach provides a reasonable method to identify conservation targets in aquatic system that can meet the goal of regional biodiversity representation, it does not assess the urgency of *threat* to such systems, an important component in conservation planning. That is, if two systems, A and B, contain similar levels of aquatic biodiversity in the same region, but A is under multiple threats of impending development and B, perhaps located in a relatively uninhabited area, is not, the strategic use of limited conservation funding would be to purchase land in the watershed surrounding A because its biodiversity is more in need of immediate protection than B. What kind of classification system could incorporate threat factors to make these kinds of conservation planning decisions? To answer that question we turn to another conservation NGO, the World Wildlife Fund.

11.2.3.2. Setting Priorities for Conservation in Freshwater Aquatic Habitats – Incorporating Threat and Urgency in Conservation Planning

The World Wildlife Fund–United States (WWF–US) recently made a priority assessment of North American lakes and streams by region using two criteria: biological distinctiveness and conservation status of watersheds within a region (Abell et al. 2000). In ranking biological distinctiveness, WWF–US gave priority to those regions that contained one or more systems that made important contributions to biodiversity at four different levels (globally outstanding, continentally outstanding, bioregionally outstanding, or nationally important). In ranking conservation status, regions were ranked as critical (intact habitat reduced to small, isolated patches with low probability of persistence over the next decade without immediate action), endangered (intact habitat of isolated patches of varying length with low to medium probability of persistence over the next 10–15 years without immediate or continuing protection or restoration), vulnerable (intact habitat remains in both large and small blocks, persistence is likely over next 10–20 years if the area receives adequate protection and restoration), relatively stable (disturbance and alteration in certain areas, but functional linkages among habitats still largely stable, surrounding landscape practices do not impair aquatic habitat or could be easily modified to reduce impacts), and relatively intact.

Priority categories I–V were assigned based on the integration of these two criteria, with priority I being the most critical and priority V being the least (Figure 11.7). Following a triage philosophy of conservation, the highest priority was given to globally outstanding areas in endangered and vulnerable status. Critical areas were considered too degraded to have high hopes of saving, and stable or intact systems were considered not to require immediate action. Within systems in the endangered and vulnerable categories, conservation priority declines as the importance of the system decreases in scope.

The WWF–US prioritization system is far from perfect, but it is useful at two different levels. As a specific prioritization of conservation needs in aquatic habitat, the assessment identifies key areas in need of immediate protection using objective criteria. As a method of conservation assessment, the ranking system can be adapted to other regions of the world or to smaller scales while preserving its intended purpose: link the priority of conservation effort to areas that will reward the effort with the greatest contribution to biodiversity. For example, conservation biologists working to manage or establish a system of local preserves may have no aquatic systems that are globally or continentally outstanding, but they may have systems that are outstanding at smaller scales, such as state or local levels. The need for such assessment, followed by appropriate management, is critical. For example, although the North

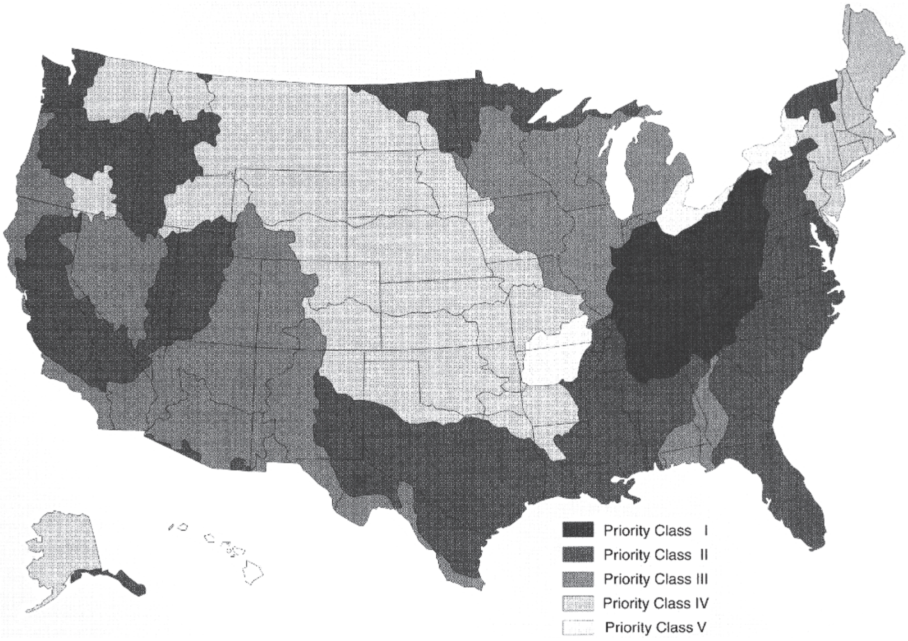


FIGURE 11.7. Priority categories for conservation of rivers, by region, in the United States developed by World Wildlife Fund–USA. Prioritization is based on combined ranking of biological value (i.e., relative contribution to global biodiversity) of the system and its current management/conservation status. Conservation efforts will vary within the same priority category due to differences between watersheds concerning the habitat, beta diversity, and resilience. (From *Freshwater Ecoregions of North America* by Robin A. Abell et al. Copyright 2000 by World Wildlife Fund. Reproduced by permission of Island Press, Washington, DC.)

American assessment found that Arctic lakes and rivers were, for the most part, intact and stable, there were no large temperate lakes or rivers that could be so described. The majority of temperate lakes and rivers were classified as endangered or critical, and thus given a higher priority for conservation protection (Abell et al. 2000).

The TNC and WWF-US strategies use a coarse-filter approach that assumes that the selected regional conservation targets will contain representative common elements of regional biodiversity. But do they? Will this type of selection also capture streams where endangered species occur, species that might select areas unrepresentative of the region as a whole? A future test for how well this kind of approach represents both biodiversity and rare species would be to examine the biodiversity and endangered species found in a portfolio of conservation areas that have been developed using regional aquatic system targets compared to one developed using species specific targets. Although we cannot yet provide a rigorous experimental comparison, we can examine the use of a fine-filter approach that has been employed in pursuit of the same goal, the preservation of regional aquatic biodiversity, and make inferential comparisons between the two strategies. Consider a case history from Spain and Portugal.

11.2.3.3. A Fine-Filter Approach to Conservation – Species Conservation Value in the Iberian Peninsula

The Guadiana River on Europe's Iberian Peninsula is currently facing the threat of radical changes in water flow regimes that would be created by the proposed development of two major hydroelectric dams, a development that could threaten many fish species native to this major river. In a collaborative effort between the University of Lisbon (Portugal) and the Hull International Fisheries Institute (United Kingdom), fish conservation scientists developed a species-by-species approach for selecting protected areas for conservation of native freshwater fishes in this area (Filipe et al. 2004). In this effort, scientists first identified native fish species present in each watershed and determined their overall distribution within the watershed based on sampling representative streams in which the species was present (Figure 11.8). Because not every stream or section of stream ("reach") could be sampled, they used the results of capture data in 1 year (1999) to construct a predictive model of species occurrence based on the relationship of species occurrence to landscape characteristics, which included climatic variables (3), geomorphological variables (4), hydrological variables such as stream flow rates and discharge (7), and variables assessing the impact of human influence (6). Using these data, they then constructed a logistic regression model for each species which determined the degree to which each variable explained variation in occurrence and abundance of each species. From this model they generated predictions of species occurrence and abundance, and then evaluated the reliability of their model by testing its predictions against samples taken in the following year (2000). The model's predictive ability was high, except for the region's rarest fish, *Anaecypris hispanica*, a species in which most of the model's predictions of occurrence were wrong. However, most model results, combined with field data, gave the scientists an accurate estimate of the proportion of stream reaches in each area in which every species was known or

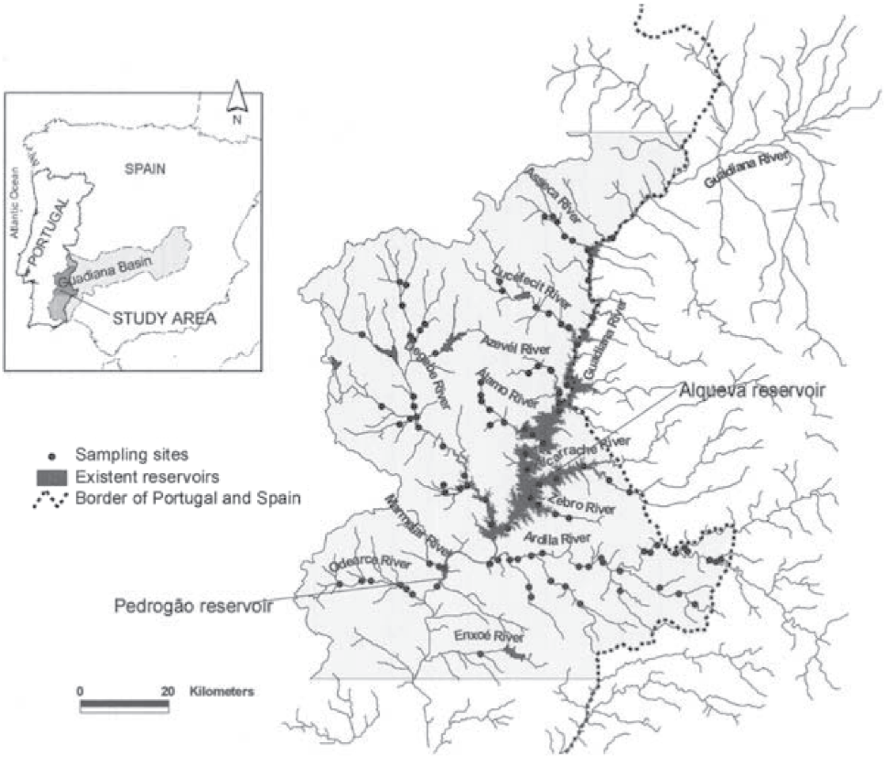


FIGURE 11.8. Major tributaries, sampling sites and existing reservoirs in the middle region of the Guadiana River Basin, Portugal. In this river basin conservation scientists used a predictive model, capture data, and knowledge of species geographic range and endemicity to determine the conservation value of every fish species and the conservation value of each stream reach based on its contribution to regional biodiversity and representation of rare endemic species. (Filipe et al., Selection of priority areas for fish conservation in the Guadiana River Basin, Iberian Peninsula, *Conservation Biology*, Copyright 2004 by Blackwell Publishing.)

likely to occur. Armed with predictable estimates of occurrence of most species in different sections of the river and its major stream tributaries, the scientists then estimated the abundance of each species based on the total number of captured individuals from all stream samples. Finally, they ranked the "endemicity" of each species based on its geographic range, with species having the most limited distributions receiving the highest score (most endemic to the region).

From these values, they were able to estimate the conservation value for each species, *k*, as VS_k through the expression

$$VS_k = \left(\left(a\frac{1/O_k}{\sum_{i=1}^{S} 1/O_i} + b\frac{1/\ln T_k}{\sum_{i=1}^{S} 1/\ln T_i} + c\frac{1/E_k}{\sum_{i=1}^{S} 1/E_i} \right) /3 \right) \times 100.$$

Although this equation looks intimidating, it expresses a fairly simply idea. *S* represents the total number of species considered and *a, b,* and *c* are weighting factors that assign a relative importance value to distribution (*a*), abundance (*b*), and endemicity (*c*) which, together, sum to a total value of 3. O_k is the total number of sampling sites where species *k* occurred in all samples (species distribution) and O_i is the sum total of all sites for every species occurrence (Filipe et al. 2004). Therefore, if a species occurred at every sampled site, the value of the first term would be 1 times *a* (the value of the weighting factor) or simply, *a*. Similarly, T_k is the total number of captured individuals of species *k* in all samples. In the extreme case that every individual in every sample was an individual of species *k*, this value also would be 1 times *b*, or *b*. E_k is the "endemic value" of species *k* based on its known regional distribution range. Again, in an extreme case, if species *k* were the only species, the value of the third part of the expression is also 1 times *c* or *c*. If all three extreme cases occurred together and, as stated, $a + b + c = 3$, then the conservation value of species *k* would be $3/3 \times 100 = 100$. The extreme case will never occur, but notice that the smaller the value of an individual species in distribution, abundance, or endemicity, the higher the score it will receive. For example, if *k* occurs in only 10 streams and the sum of all occurrences of all species is 100 streams, then the first part of the equation is *a* (0.1/0.01) or 10*a*. In this way, the rarer the species is in distribution, abundance, or endemicity, the higher its conservation score. In this particular case, the researchers assigned twice as much weight to distribution and abundance (*a* and *b* each equal 1.2) than to endemicity ($c = 0.6$) because, in this effort, the conservation goal was to select priority streams at a regional level. That is, the goal was to select species that were regionally low in distribution and abundance, with less emphasis on whether they were abundant or rare at continental levels. This emphasis makes sense in a conservation strategy that is designed to preserve the fish biodiversity of the Iberian Peninsula, not simply continental or global fish biodiversity.

The second step, using the conservation value of each species, to then assign a conservation value to each given area, *j*, within the watershed, or VA_j, calculated as the sum of the products of the probability of occurrence of each species in each area, or

$$VA_j = \sum_{k=1}^{S} (P_{kj} \times VS_k),$$

where P_{kj} is the probability of occurrence of the now familiar species *k* in area *j* and VS_k is the previously calculated value of species *k* (Filipe et al. 2004). Thus, the outcome of this methodology is that the area in the watershed whose streams have the greatest probability of holding species of limited regional distribution, low regional abundance, and high endemicity will be the area that receives the highest score in conservation value and will be placed first on the list of priority areas to be conserved, and every species in the watershed can be ranked with a unique conservation value (Table 11.1).

To identify reserves, these researchers used a threshold that maximized the conservation value of each stream reach but identified a minimum number of reaches that would constitute an appropriate reserve. In other words, if an area had high conservation scores for all of its stream reaches, but had too few reaches to achieve the threshold, it would not be considered for protection because it would not contain enough streams to make the protection worthwhile. Based on this information, these scientists were able to determine both the best streams to conserve and the total proportion of stream reaches to be conserved to protect most of the regional fish biodiversity.

This species-specific approach yields a more defined picture of what will actually be conserved in specific reaches than TNC's or WWF-US's coarse-filter strategies of bioregional representation, and permits estimation of specific conservation values of individual streams and stream sections. It is also labor intensive and region specific. The method could not be used elsewhere without a similar sampling effort and model construction for each species in the new region. For worldwide conservation, TNC's and WWF-US's coarse-filter approaches have the advantage of more economical and more rapid applicability in making conservation decisions for freshwater ecosystems. But where data are sufficiently detailed or time permits such data to be collected, the approach of Filipe et al. (2004) provides a greater level of precision in conservation decision making and less uncertainty about how to conserve fish species of high conservation value.

11.3. Wetlands – Unique Challenges in Habitat Conservation

11.3.1. What Are Wetlands?

Wetlands*,* have been defined as *lands transitional between terrestrial and aquatic systems where the water table is at or near the surface or the land is covered by shallow water* (Cowardin et al. 1979). Wetlands make disproportionately large contributions to global biodiversity and primary productivity. They often harbor disproportionately high numbers of endangered species, game species, and other economically important species. But because many wetland areas are transitory or ephemeral in nature, both their definition and their dynamics make it difficult to estimate the exact extent of wetlands in the world today. Not surprisingly then, worldwide estimates vary from 5.3 million square kilometers (Matthews and Fung 1987) to 8.6 million square kilometers (Maltby and Turner 1983).

As habitats and ecosystems, wetlands provide services and products far in excess of the approximately 6% of the earth's surface they cover (Matthews and Fung 1987; Gosselink and Maltby 1990). Like an economic entity whose value is made up of assets, services, and attributes, wetlands have value in their assets of structural components, the services provided by their environmental functions, and the attributes of their system organization (Barbier 1995).

In components, wetlands provide species that form the basis of many sport and commercial fishing industries,

TABLE 11.1. Conservation value (*VS*) for each of the native freshwater fish species in the middle region of the Guardiana River Basin (Spain and Portugal) and the data used to derive the value.

Species	No. of sampling sites with occurrence	No. of captured individuals	Endemic value[a]	VS
Anaecypris hispanica	7	58	1	22.68
Barbus comizo	14	37	3	14.33
Chondrostoma lemmingii	24	554	2	9.38
Salaria fluviatilis	24	274	4	8.94
Chondrostoma willkommii	26	352	1	11.15
Barbus microcephalus	48	1,032	1	8.89
Squalius pyrenaicus	38	576	3	7.32
Cobitis paludica	60	874	3	6.19
Barbus steindachneri/sclateri	66	2,553	2	6.18
Squalius alburnoides complex	79	8,581	3	4.95

Source: Filipe et al., Selection of priority areas for fish conservation in the Guadiana River Basin, Iberian Peninsula, *Conservation Biology*, Copyright 2004 by Blackwell Publishing.

[a] Endemism value of the species according to its distributional range: 1, Guadiana endemic; 2, Meridional Sector of Iberian Peninsula endemic; 3, Iberian endemic; 4, Circum-Mediterranean endemic.

hunting, and agriculture (for example, various forms of domestic and wild rice), as well as wildlife products (especially fur and meat), wood, and water (Barbier 1995). In fact, most game and fur-bearing animals in temperate regions, and many species of game fish spend at least part of their life cycle or at least one season of the year in wetlands, even if they are not "wetland species." A disproportionate number of threatened and endangered species also are wetland dependent.

In services, wetland functions are varied and essential. For example, because wetlands have the capacity to absorb large inputs of water from surface runoff or upstream sources and yet release relatively little of these inputs downstream in the short-term, intact wetland systems protect downstream landscapes, natural systems, and human communities from storm and flood damage. Because wetlands contain dense, highly productive plant communities they can absorb large quantities of waste and nutrient runoff. Wetlands also provide opportunities for many types of recreation and water transport. Other wetland services are provided by "constructed wetlands," which are the products of human engineering for specific purposes. Constructed wetlands are created where wetlands did not previously exist or where the original wetlands were destroyed or degraded. The most common type of constructed wetland is designed for wastewater treatment (Brix 1994), but wetlands also are constructed for wildlife habitat, research, and as compensation for loss of natural wetlands.

Wetland organizational characteristics support high levels of primary productivity and biomass. Because water is shallow throughout the wetland environment, all parts of the system can be photosynthetically active, unlike deepwater environments where light cannot penetrate below certain depths. Because water levels vary spatially and temporally (seasonally) within a wetland, the environment experiences strong moisture gradients that support a diversity of plant life, including plants of diverse life- and growth-forms. Such plant diversity creates physical heterogeneity and complexity greater than most terrestrial environments, and often supports a correspondingly more diverse biotic community.

11.3.2. Managing Wetlands for Conservation – Management and Legislation

Vegetative buffer strips adjacent to wetlands, even if relatively monotypic and composed of common, inexpensive grass species, remove nutrients, including nitrates and phosphates, from runoff and permit fewer nutrients to enter the wetland than if the wetland were not buffered (Rickerl et al. 2000). An interesting and unexpected outcome of planting buffering vegetation is that it may actually increase the diversity of the plant community around the aquatic system. In South Dakota (USA), three species – smooth bromegrass (*Bromus inermis*), orchardgrass (*Dactylis glomerata*), and alfalfa (*Medicago sativa*) – were planted as buffer species in experimental plots around wetlands. After establishment, the buffered communities had 29 additional plant species not found in the wetland itself or in uplands around unbuffered wetlands (Rickerl et al. 2000).

Coordinated management of lake-wetland complexes can produce more effective results for conservation than managing each system separately. Managers can reduce the inputs of phosphorus and other nutrients into a lake by maintaining or creating wetlands around it. Wetland vegetation and associated wetland systems absorb greater quantities of nutrients, especially phosphorus and nitrates, entering a lake's drainage basin than can terrestrial vegetation. Wetlands can remove up to 79% of total nitrogen, 82% of nitrates, 81% of total phosphorus, and 92% of sediment in drainage water (Chescheir et al. 1992). Wetlands, as noted earlier, often provide disproportionately high levels of species richness compared to terrestrial or aquatic habitats of similar area. In many cases of island flora and fauna, as the size of a given type of wetland increases, so does its species richness. Thus the conservation value of many types of wetlands may increase with size (Findlay and Houlahan 1997), although this is not the case for all wetlands, such as vernal pools, small bogs, and prairie potholes which may harbor specialist species not found in larger wetlands. Because wetlands are often radically different than their surrounding landscape, successful management of wetland species may require management of landscape level processes that extend far from the wetland's borders. For example, Findlay and Houlahan (1997) determined that wetland species richness in plants, herptiles (amphibians and reptiles), and birds was negatively correlated with the density of paved roads within 2 km of the wetland edge and species richness in plants, herptiles, and mammals was positively correlated with the proportion of forest cover within the same distance in wetlands in southeastern Ontario (Canada). Thus, a manager may be able to enhance biodiversity in a wetland as much by managing land use processes around it as by managing the wetland itself.

Many aquatic and wetland species show dramatic shifts in distribution over relatively short-time spans. Managers must determine if such changes represent the effects of habitat loss or environmental change or are simply random events. Making an accurate determination is critical to making an appropriate management response. But managers cannot make these determinations without systematic assessment and decision-making processes. One approach to making such assessments is the use of so-called ***rule-based models*** that evaluate possible mechanisms of distributional changes in species. Skelly and Meir (1997) used a rule-based approach to evaluate possible causes of changes in distributions of 14 species of amphibians across a landscape of 32 ponds in Michigan (USA). Specifically, they attempted to explain changes using three different models: (1) an ***isolation model*** that assumed that changes in distribution were driven by distances between ponds (i.e., by dispersal abilities of the amphibians); (2) a ***succession model*** that assumed that distribution was determined by changes in vegetation in and around the ponds; and a (3) ***null model*** that assumed that changes were random events. Their basic data set consisted of presence-absence data of 14 amphibian species based on annual amphibian surveys from 1967 to 1974 and 1988 to 1992. The underlying hypothesis of each model was used to divide the ponds into three classes based on (1) distance of the pond to its nearest population of each species (isolation model); (2) vegetational characteristics in and around the pond (succession model); or (3) random assignment of each pond to one of three classes (null model). For individual species, the succession model made fewer mistakes predicting occurrence of three species at individual ponds and was better at predicting overall species richness at ponds (Skelly and Meir 1997).

These results suggested that the presence of amphibians in this landscape of wetlands could be best managed by managing the vegetation characteristics of the ponds, not by changing the distribution of ponds. Skelly and Meir note that the ability to explain a pattern with a rule-based model is not the same as showing causation between a factor and its effect. To accomplish that, managers would have to manipulate vegetation in and around the ponds experimentally and monitor amphibian response. What the rule-based approach does provide is insight about *which* experiments might be most useful to conduct. The authors conclude that "even relatively coarse information on presence and absence can be put to an … important use: as survey information accumulates it becomes a source of insight for managers interested in determining *why* species distributions are changing, not just *if* they are changing" (Skelly and Meir 1997). Rule-based models can be used in contexts other than wetland species. But their application here shows how a manager, informed only by simple survey data, could use rule-based models to evaluate different courses of management actions and plan definitive experiments to understand the causes of changes in wetland species presence and distribution.

Wetlands were one of the first cases in which international legislation, the Ramsar Convention, focused on the protection of an ecosystem instead of a species, and national legislation and global treaties and conventions remain critical elements in wetland conservation and management. The Ramsar Convention obligated its signers to land-use planning for wetlands and wetland preservation, to identifying and designating at least one wetland in their country as a "wetland of international importance," and to establishing wetland nature reserves (Koester 1989). Canada's federal policy on wetland conservation provides one of the best national examples of implementing the ideals of Ramsar. The Canadian policy is a comprehensive federal plan that articulates strategies for sustainable use and management of the nation's wetlands. It aims to provide for the maintenance of overall wetland function on a national level; enhance and rehabilitate degraded wetlands; recognize wetland functions in planning, management, and economic decision making in all federal programs; secure and protect wetlands of national importance; use wetlands in a sustainable manner; and allow no net loss of wetlands on federal lands and waters (Rubec 1994). Although no policy is ever perfectly translated into practice, the Canadian wetlands policy has experienced remarkable success, primarily through its non-regulatory approach. Each Canadian province, following directives of federal policy, has developed its own public review and consultation process for wetland conservation (Rubec 1994). Federal wetland directives led to the publication of a standardized manual, the *Wetlands Evaluation Guide* (Bond et al. 1992). With an estimated endowment of nearly one-quarter of the world's remaining wetlands, Canada's leadership in federal wetlands policy is not only commendable but strategic, especially considering that Canada is estimated to have lost approximately one-seventh of its historic wetlands (Rubec 1994).

11.4. Marine Habitats and Biodiversity

11.4.1. A History of Overexploitation

Although problems of marine habitat and species preservation show expected local and regional variation, the major threats to marine environments are consistent through the world. Some are similar to threats facing freshwater environments, whereas others are unique to marine systems. The most important global threats include exploitation of commercial species, direct destruction of marine habitats, indirect degradation of marine habitats from land-based sources including eutrophication, pollution (primarily from radioactive wastes, heavy metals, and petroleum products), the degradation of coastal zones (from erosion, development, and habitat destruction) (Van DeVeer 2000), and nonindigenous species (Ruiz et al. 1997).

In the 1940s and 1950s, the emerging science of fisheries management perceived fish stocks as renewable resources that could be managed for maximum sustainable yield (MSY), a value that could be calculated precisely by various means, primarily using estimates based on catch per unit effort (Ricker 1958). All that was thought to be required for a sustainable fishery was reproductive surplus. Today the concept of MSY has all but disappeared from fisheries science, along with many of the fish stocks mismanaged under its assumptions. Biologists have gradually learned that most fish populations (1) show wide fluctuations of high and low abundance; (2) do not necessarily show a strong correlation between recruitment and number of adults present; and (3) do not necessarily show advance warning of impending population decline or crash from overexploitation (Hilborn et al. 1995). Rather, declines may be sudden, and stocks may not recover in the short-term even when given complete protection.

The effects of over-exploitation on targeted commercial species are not surprising, but the effects on non-target species can be equally devastating. The removal of prey species can reduce populations of predator species, and not of fish only, but also of birds and mammals. Examples have been seen in the decline of Peruvian seabirds following the decimation of the anchovy fishery and the decline of sea otter populations off the California coast following overfishing of abalones (Agardy 1997).

Some cases have had legal as well as biological ramifications. In 1998, a coalition of US environmental organizations sued the North Pacific Fishery Management Council under the US Endangered Species Act for failing to protect foraging habitat for the Stellar sea lion by allowing unregulated pollock (*Theragra chalcogramma*) fishing in the sea lion's foraging areas (Stump 2000). Lack of food had previously been identified as a cause of decline in sea lion populations, and pollock is an important prey of sea lions. The plaintiffs argued that it made no sense to allow unregulated fishing in critical foraging habitat, and that such fishing violated the ESA's directive that "reasonable and prudent alternative (RPA) measures" be taken to avoid inflicting "adverse modification" on critical habitat of a species. A US district court upheld the decision and ordered the National Marine Fisheries Service to revise its RPA (Stump 2000).

The Stellar sea lion, in the previous example, was harmed by reductions in its prey populations, but all marine mammal species throughout the world also are victims of direct mortality as ***bycatch***, especially in the form of pinnipeds, like sea lions, and cetaceans that are caught in gill nets. Andrew Read of Duke University's Marine Laboratory and his colleagues, after an extensive review and analysis, estimated that annual bycatch mortality of marine mammals, excluding sirenians (manatees) and sea otters, in the US alone was 6,215 ± 448 from 1990 to 1999, although it declined significantly after reduction measures were enforced in the US in the second half of this decade (Table 11.2) (Read et al. 2006). Measures of global bycatch are less precise, but, using US ratios of catch/vessel, Read et al. estimated global bycatch mortality of marine mammals in the hundreds of thousands (Table 11.3) (Read et al. 2006).

TABLE 11.2. Estimates of marine mammal bycatch in US fisheries stratified by taxon and fishery type, 1990–1999.

Taxon and fishery type	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
Cetaceans										
Gill net	4,902	3,154	2,373	2,489	2,928	2,261	2,624	2,095	1,481	1,051
Trawl	195	297	232	133	199	195	999	436	116	332
Other	3	9	256	60	388	475	114	11	70	408
Pinnipeds										
Gill net	1,921	3,312	5,626	3,573	3,540	3,136	2,472	2,873	2,323	2,344
Trawl	19	36	34	10	29	3	15	17	14	11
Other	151	149	148	10	29	30	6	20	15	0

Source: Read et al. Bycatch of marine mammals in the U.S. and global fisheries, *Conservation Biology*, Copyright 2006 by Blackwell Publishing.

TABLE 11.3. Estimates of marine mammal bycatch in global fisheries, 1990–1994. Estimates based on extrapolation of US bycatch per vessel ratios to total number of world fishing vessels.

Fishery type and year	No. of US vessels	Total no. of vessels	Global cetacean bycatch	Global pinniped bycatch	Global marine mammal bycatch
Gill net					
1990	2,140	203,598	466,392	182,763	649,154
1991	2,140	217,585	320,633	336,748	657,381
1992	2,160	218,272	239,766	568,518	808,283
1993	2,500	219,461	218,513	313,654	532,167
1994	2,500	220,500	258,250	312,228	570,478
Trawl					
1990	7,446	129,403	3,389	330	3,719
1991	7,440	130,128	5,198	630	5,828
1992	8,150	132,957	3,790	555	4,344
1993	8,290	137,720	2,213	166	2,379
1994	8,030	137,479	3,407	496	3,904
Other					
1990	3,220	77,640	72	3,645	3,717
1991	3,180	79,045	222	3,708	3,930
1992	3,230	80,606	6,382	3,698	10,079
1993	3,495	80,366	1,377	235	1,612
1994	3,430	80,991	9,164	685	9,849

Source: Read et al. Bycatch of marine mammals in the U.S. and global fisheries, *Conservation Biology*, Copyright 2006 by Blackwell Publishing.

As the removal of a prey species can cause declines in the predator, so the removal of predator can cause changes in prey populations, and those changes do not always lead to uniform or long-term increases. Over-exploitation disrupts equilibria of many populations (Agardy 1997), and can make them more susceptible to declines associated with environmental and demographic stochasticity (Chapter 8), such that stocks may continue to decline even after take is restricted or stopped altogether (Lauck et al. 1998). As with marine mammals, the take of other kinds of non-targeted species in commercial fishing also continues to be a serious problem despite concern, attention, legislation, and supposedly improved technologies. In some fisheries, such as shrimp, the discarded biomass of bycatch exceeds the targeted catch worldwide (Agardy 1997). Species such as sea turtles, dolphins, sharks, rays, and benthic organisms continue to be killed in large numbers as by-catch species.

Exploited as they are, marine ecosystems show resiliency when given opportunity to recover. Among the large marine ecosystems of the world, the US Northeast Shelf Ecosystem has historically been one of the most productive, and most heavily exploited, of all ocean fisheries. Stocks in this fishery had become so depleted by the 1990s that, by 1994, days-at-sea for fishing trawlers were reduced to 50% of pre-1994 levels (Sherman et al. 2003). The problem was especially acute among bottom-dwelling species or ***demersal species***, so-called "groundfish" such as flounder and haddock, and became so serious that government and private industry began to cooperate more effectively than ever before to save the fishery. Changes resulting from that cooperation were sweeping. Four areas containing over 5,000 nautical miles were closed to vessels with fishing gear capable of catching groundfish. New regulations increased minimum net mesh size (allowing younger individuals to escape), a moratorium was placed on new vessel entrants (i.e., no new fishing vessels allowed to enter the industry), and vessel and dealer reporting of catches became mandated. Total allowable catch levels (TACs) for species identified as "depleted" were significantly reduced. Going further, the US Congress approved a plan for buying out 79 groundfishing vessels from their owners, thus, further reducing fishing effort (Sherman et al. 2003). With the passage of the US Sustainable Fisheries Act in 1996, even more restrictions were imposed. But could an exploited stock recover, or was such effort still too little too late? Remarkably, stocks of demersal species showed rapid recovery in this system (Figure 11.9), and stocks of ***pelagic*** (free-swimming, upper layer) ***species*** such as herring and mackerel also have risen as reductions in fishing effort and TAC have been implemented (Sherman et al. 2003).

11.4.2. Causes of Marine Habitat Degradation

Just as marine populations can be destroyed by overharvest, they also can be destroyed, like their terrestrial counterparts, by habitat destruction. The destruction of marine habitats, especially benthic (bottom) habitats, can occur through a variety of means, most of which are associated with commercial fishing, and all of which can represent significant threats to global biodiversity.

Of 29 nonsymbiont animal phyla known on earth, all but one have representatives in the ocean, and all of these have representatives in benthic communities. In fact, most of the diversity found in marine ecosystems consists of invertebrates that live in or on bottom sediments (Snelgrove 1999). We are only now beginning to appreciate the biodiversity of such communities. For example, 64% of polychaete (tubeworm) taxa identified in one deep-sea study were previously unknown to science (Grassle and Maciolek 1992). Given such ignorance, it is not surprising that we do not know the exact number of marine benthic species, but estimates have ranged from a low of 500,000 (May 1992) to a high of more than 100 million (Lambshead 1993). There is enormous variability in benthic habitats and their associated communities, but some general patterns hold worldwide. Benthic habitats in extreme environments, such as estuaries, eutrophied areas, and high-energy regions with low organic content, have lower diversity than sediments in aquatic habitats without these characteristics (Snelgrove 1999). Diversity in sediment grain size is directly correlated with the diversity of the benthic community, probably because a greater diversity of sediment sizes provides a higher diversity in sizes of food particles (Whitlatch 1977). Finally, diversity in seagrass bed sediments is higher than in adjacent sediments associated with open areas (Peterson 1979).

The structure of benthic communities is altered by the use of bottom trawling nets (Figure 11.10). Auster (1998) provides a picture of a location on the bottom of the Gulf of Maine off the East Coast of the United States before and after bottom trawling. The top photographs (before) reveal a complex and diverse assemblage of creatures, including tubeworms, sponges, and many other forms of life. The bottom photographs (after) show the same spot after a trawl net was dragged across it. The complexity of the habitat has been obliterated, along with all its residents.

This vivid, visual example of marine habitat destruction can be understood more generally through a conceptual model of the effects of fishing gear upon different marine habitats, such as might be found on a continental shelf. Consider eight different categories, ranging, at the simplest level, from flat sand or mud to the most complex, piled boulders (Table 11.4). Auster (1998) assigned a "numerical complexity score" to each habitat category. Note that, as habitats become more complex, scores do not increase linearly. For example, category 6, pebble-cobble with sponge cover, receives five (not one) additional points because it contains elements of all previous

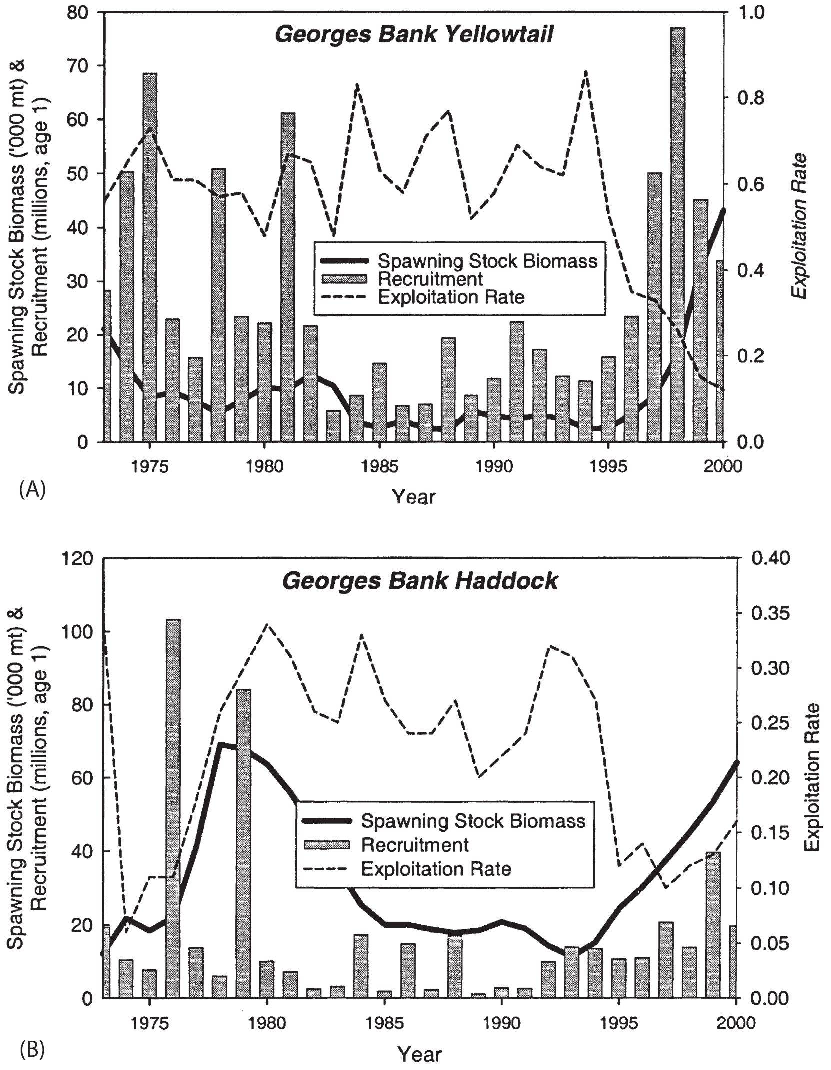


FIGURE 11.9. Recovery of yellowtail flounder (A) and haddock (B) from the Georges Banks/ US Northeast Shelf Ecosystem following reductions in total allowable catch and gear restrictions. Note that stock biomass and recruitment in both species began to recover almost immediately after reduction in exploitation rate. (Sherman et al. 2003:93–120. Copyright 2003. With permission of Elsevier.)

categories plus dense emergent epifauna. Category 7 receives ten points for containing all the elements of category 6 plus two points for shallow boulder crevices and current refuges. Finally, category 8 receives an additional three points for its addition of deep crevices (Auster 1998). The effect of intensive fishing activity, primarily trawls and dredges, is to reduce habitat complexity by smoothing bedforms (habitat categories 1 and 2), removing epifauna (categories 3, 4, and 6) and removing or dispersing physical structures (categories 5, 7 and 8). Such a model predicts that the effect of fishing activity on habitat complexity is nonlinear (Figure 11.11). The more complex the original habitat, the greater the loss of complexity that results (Auster 1998).

Marine habitats are even more degraded from land-based sources. This indirect, but extensive degradation has multiple causative agents (Table 11.5). Many of these, such as eutrophication, sedimentation, and thermal pollution, are proximity-based relative to the source of the pollution, and thus have their greatest effects on coastal and estuarine environments. But others, such as radioactive wastes and persistent toxins such as PCBs, DDT, and similar compounds, travel long-distances in ocean currents, or may be deposited far out to sea through atmospheric circulation patterns. Likewise, some kinds of military wastes like radioactive material or chemical weapons may be transported long distances from shore before being deposited. These pollutants can cause habitat destruction and devastate populations thousands of miles from their source of origin.

As in freshwater and terrestrial habitats, non-indigenous species pose a significant threat to the stability and marine communities and the habitats that support them. Historically, most invasions were by so-called "fouling

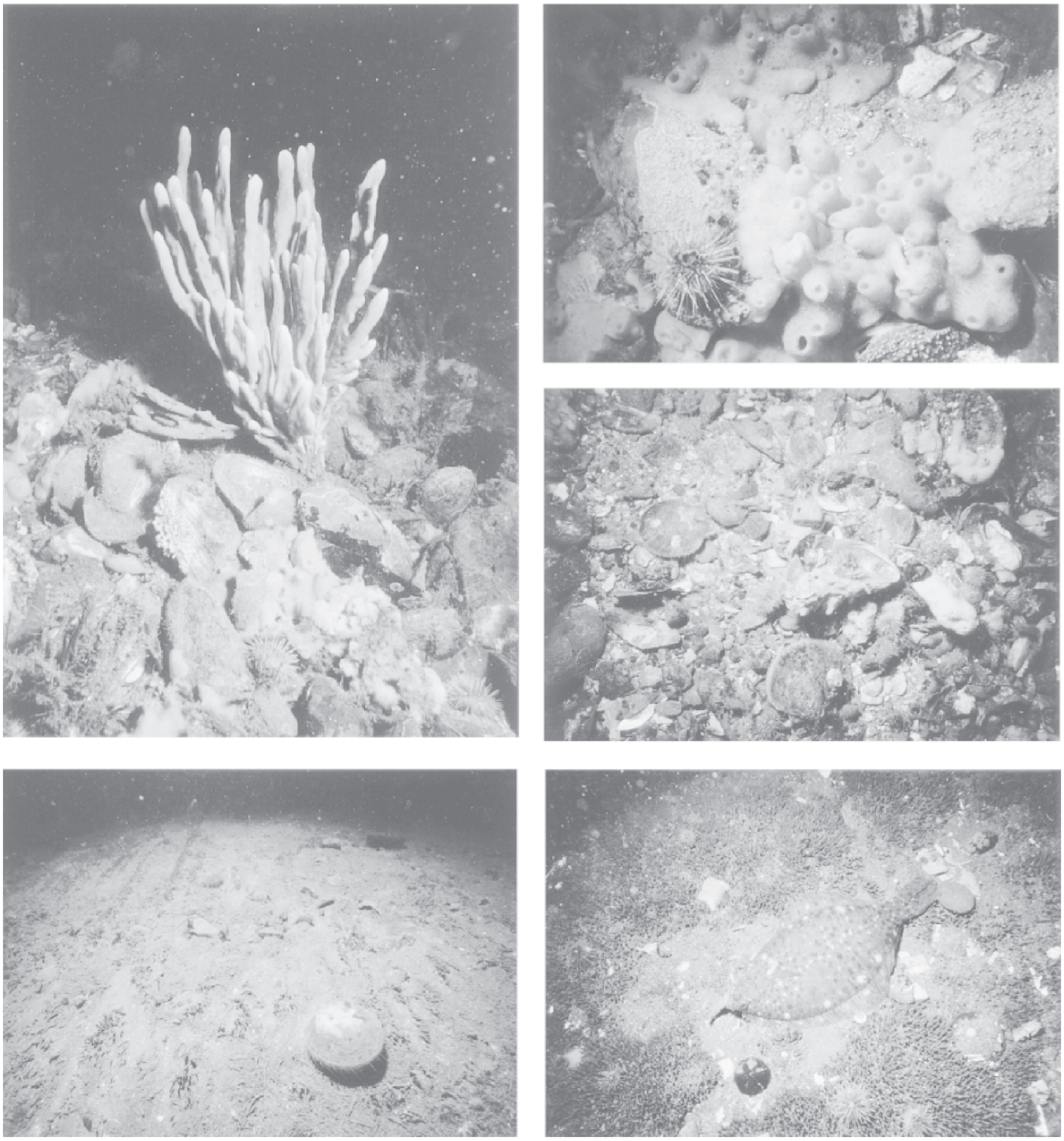


FIGURE 11.10. A portion of the Atlantic Ocean bottom before (top) and after (bottom) being swept by a trawler net. Note that, prior to trawling, a complex and diverse community is present in and on the sediments. After trawling, it has been obliterated. (Auster, A conceptual model of the impacts of fishing gear on the integrity of fish habitats, *Conservation Biology*, Copyright 1998 by Blackwell Publishing.)

organisms" that attached themselves to the hulls of ships (Ruiz et al. 1997). Today, as metal hulls have replaced wooden ones and the speed of ocean vessels has increased, these types of invaders have actually declined in importance, but, four other means of invasion remain. These include (1) intentional releases of aquaculture, commercial or sport fishery or bait species; (2) the connection of waterways through canals; (3) the release of species associated with the pet industry of with other types of management practices, such as releasing invasive species for the biological control of other pest species; and (4) the release of organisms in the ballast water of ships. Of these, the last has often been the most destructive to native communities and habitats, perhaps because it is the least intentional yet introduces the largest volume of water into new areas. For example, in the San Francisco Bay Delta ecosystem (USA), one of the world's busiest ports, there are now over 200 non-indigenous species in residence, making this delta the most heavily invaded estuary in the world, to the point that today nearly all macroinvertebrates found along the inner shoals of this delta are non-indgenous species. And just one non-indigenous species, the Asian clam, has reached densities of up to 30,000 individuals/m^2 in some locations, disrupting planktonic and benthic communities as well as assemblages of finfish, and costing

TABLE 11.4. A classification of fish habitat types on the outer continental shelf of the temperate northwest Atlantic. Note that habitat complexity scores do not increase at a constant rate, but reflect cumulative effects of structural components added at each succeeding level.

Category	Description[a]	Rationale	Complexity score
1	Flat sand and mud	Areas with no vertical structure such as depressions, ripples, or epifauna	1
2	Sand waves	Troughs provide shelter from current; previous observations indicate that species such as silver hake hold position on the downcurrent sides of sand waves and ambush drifting demersal zooplankton and shrimp	2
3	Biogenic structures	Burrows, depressions, cerianthid anenomes, hydroid patches; features that are created or used by mobile fauna for shelter	3
4	Shell aggregates	Provide complex interstitial spaces for shelter; also provide a complex, high-contrast background that may confuse visual predators	4
5	Pebble-cobble	Provide small interstitial spaces and may be equivalent in shelter value to shell aggregate, but less ephemeral than shell	5
6	Pebble-cobble with sponge cover	Attached fauna such as sponges provide additional spatial complexity for a wider range of size classes of mobile organisms	10
7	Partially buried or dispersed boulders	Partially buried boulders exhibit high vertical relief; dispersed boulders on cobble pavement provide simple crevices; the shelter value of this type of habitat may be less or greater than previous types based on the size class and behavior of associated species	12
8	Piled boulders	Provide deep interstitial spaces of variable sizes	15

[a] Classification is based on Auster et al. (1995, 1996), Langton et al. (1995), and unpublished observations

Source: Auster, A conceptual model of the impacts of fishing gear on the integrity of fish habitats, *Conservation Biology*, Copyright 1998 by Blackwell Publishing.

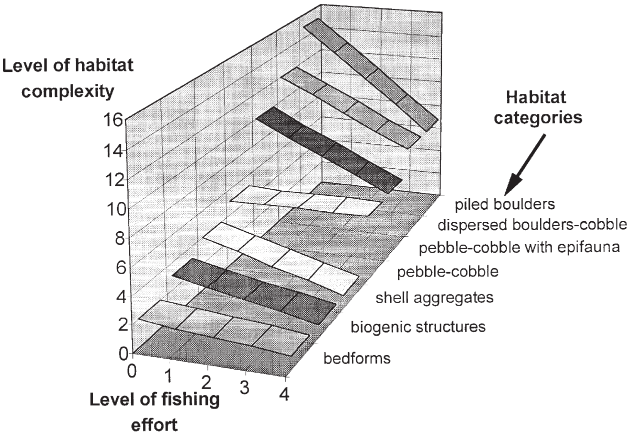


FIGURE 11.11. A conceptual model of the effects of fishing gear on sea floor habitat. Note that increases in fishing effort produce disproportionately greater reductions in habitat complexity in complex habitats compared to simpler habitats. (Auster, A conceptual model of the impacts of fishing gear on the integrity of fish habitats, *Conservation Biology*, Copyright 1998 by Blackwell Publishing.)

US$1 billion per year in damages and posing a significant threat to bay's overall ecological health (Kennish 2004).

The intentional releases of some species have occasionally brought important new sources of commercial and sport fishing or aquaculture. For example, the Pacific oyster (*Crassostrea gigas*) was brought from Japan to San Francisco Bay to establish an oyster fishery there, and that effort was successful. Other planned introductions, however, have had unforeseen and sometimes devastating consequences. The connection of different marine environments by canals has allowed two-way invasions between established communities in different areas, sometimes from radically different environments. Today the Mediterranean Sea has over 240 exotic species, and 75% are attributed to migration through the Suez Canal, primarily from the Red Sea (Ruiz et al. 1997).

The most extensive and common mechanism of invading species is through the ballast water of ships. One ship can carry more than 150,000 metric tons of ballast water for trim and stability, which it may dump in an estuary at the end of a voyage. In estuaries associated with major port systems, the amount of water dumped from foreign oceans can be staggering. For example, the port system of the Chesapeake Bay (USA) has been estimated to receive over 10 million metric tons annually, and US and Australian ports combined may receive over 79 million metric tons each year (Ruiz et al. 1997). This amounts to more than nine million liters of water per hour! At this rate of input, it is not surprising that estuaries receive more exotic invaders than open oceans. For example, 212 non-indigenous species are known from San Francisco Bay, but fewer than ten have been found along its adjoining outer coast (Ruiz et al. 1997).

Although invasions in freshwater systems are notorious for their devastating results on native species, marine environments and communities appear to be more resistant. The US Fish and Wildlife Service considers exotic species to be a significant cause of decline of 160 native threatened or endangered species in the United States, but few of these are marine. In fact, there are relatively few recent extinctions of marine and estuarine species, and these extinctions did not appear to be caused by exotic species. Nevertheless, some exotic species have devastated native populations, marine environments, and commercial fisheries. The recent invasion of San Francisco Bay by the Asian clam has altered marine communities in ways similar to the effects of the zebra mussel on freshwater systems (Chapter 9).

TABLE 11.5. Some types of land-based pollutants that degrade marine habitats and ecosystems.

Herbicides	• May interfere with basic food chain processes by destroying or damaging zooxanthellae in coral, free living phytoplankton, algal, or seagrass communities. • Can have serious effects even at very low concentrations.
Pesticides	• May selectively destroy or damage elements of zooplankton or benthic communities; planktonic larvae are particularly vulnerable. • May through accumulation in animal tissues have effects on physiological processes such as growth, reproduction, and metabolism. • May cause immediate or delayed death of vulnerable species.
Antifouling paints and agents	• May selectively destroy or damage elements of zooplankton or benthic communities. • Likely to be a significant factor in harbors, near shipping lanes, and in enclosed, poorly mixed areas with heavy recreational boat use.
Sediments and turbidity	• May smother substrate. • May smother and exceed the clearing capacity of benthic animals, particularly filter feeders. • Reduce light penetration, likely to alter vertical distribution of plants and animals in shallow communities such as coral reefs. • May adsorb and transport other pollutants.
Petroleum hydrocarbons	• A wide range of damaging effects depending upon type of hydrocarbon, dilution, weathering, dispersion, emulsification or interaction with seawater or other chemicals. • Direct contact with living tissue usually results in local necrosis and, with longer exposure, death. • Exposure to water-soluble hydrocarbons results in mucus production, abnormal feeding, changes to a wide range of physiological functions, and with longer exposure, death. • Detrimental effects on reproduction and dispersion; premature discharge of larvae, distorted larvae, decreased larval viability. • Residual hydrocarbons in substrates may lead settling larvae to avoid affected areas, and thus block recolonization and repair.
Sewage-detergent phosphates	• Inhibit a wide range of physiological processes and increase vulnerability of affected biota to a range of natural and human induced impacts. • Inhibit calcification, e.g., in corals and coralline algae. • Can cause effects at very low levels.
Sewage and fertilizers – nitrogen	• Increased primary production in phytoplankton and benthic algae distorts competitive and predator/prey interactions in biological communities in areas such as coral reefs, which are characterized by very low natural nitrogen levels. • Reduced light penetration through absorption and turbidity of increased planktonic communities. • Increased sedimentation of detritus from planktonic communities. • Increased nutrient levels in benthos from sedimentary organic material. • Selectively favors growth of some filter or detritus feeders such as sponges and some holothurians. • Some species such as corals are affected at very low levels.
High or low salinity water – freshwater runoff, effluents	• Low salinity water floats on top of water column, high salinity water sinks, prior to mixing and dispersion. • Tolerance of species highly variable so changed regime may alter biological communities, particularly those in shallow, poorly mixed or enclosed waters. • Salinity is a key factor in settlement and physiological performance of many shallow benthic and reef organisms. • May (e.g., for corals) cause physiological stress evidenced by elevated mucus production, expulsion of zooxanthellae, or death.
High or low temperature water – from industrial plant heating or cooling	• Tolerance of species highly variable so changed regime may alter biological communities, particularly those in shallow, poorly mixed or enclosed waters. • Temperature is a key factor in settlement and physiological performance of many shallow benthic and reef organisms. • May (e.g., for corals) cause physiological stress evidenced by elevated mucus production, expulsion of zooxanthellae, or death.
Heavy metals, e.g., mercury, cadmium	• May be accumulated by, and have severe effects upon, filter feeders and, by accumulation up the food chain, pass these effects to higher predators. • Can interfere with physiological processes such as the deposition of calcium in skeletal tissue. • May (e.g., for corals) cause physiological stress evidenced by elevated mucus production, expulsion of zooxanthellae, or death.
Surfactants and dispersants	• Most are toxic to marine biota. • Synergistic effects of dispersant/hydrocarbon mixes can be more toxic than either component unmixed. • Can interfere with a wide range of physiological processes, e.g., photosynthesis.
Chlorine	• At low levels inhibits external fertilization of some invertebrates, e.g., sea urchins. • Can be lethal to many species.

Source: Kenchington (1990).

The Asian clam has become so numerically dominant, achieving densities of over 10,000 individuals/m^2, that it has replaced other benthic organisms, cleared plankton from overlying water, and eliminated seasonal plankton blooms (Snelgrove 1999). The American comb jelly (*Mnemiopsis leidyi*) has contributed to a collapse of commercial fisheries in the Black and Azov Seas in Europe because it competes more effectively for the same food source (copepods) as native commercial fish (Ruiz et al. 1997).

Marine invasions are not as well studied or understood as those that occur in terrestrial habitats or in freshwater, so it is still difficult to identify general trends or effects common to most invaders. There is evidence that, in the long run, invading species decrease the abundance and diversity among remaining native species, that they decrease variation among communities (reduction in beta diversity, Chapter 4), and that they may alter gene flow within and among communities (Ruiz et al. 1997).

11.4.3. Threats to Coral Reef Ecosystems

Coral reefs have been called the tropical rainforests of the oceans. Worldwide over 600 species of coral contribute to this remarkable habitat, and individual reefs may harbor up to 400 species of coral, 1,500 species of fishes, 4,000 different species of mollusks and 400 species of sponges (Hinrichsen 1997). Although the bulk of any coral reef is non-living matter, the surface layer of living creatures is composed mostly of coral polyps. Relatives of jellyfish and anemones, the polyps have column-shaped bodies topped with stinging tentacles. These creatures secrete calcium carbonate as a metabolic product, and from such secretions fashion cup-shaped structures that serve as their homes and that they attach to one another. Over many years and generations of coral these calcium carbonate secretions build a coral reef, each new generation enlarging the reef by building on the bodies of their departed ancestors.

Coral reefs are centers of biodiversity because they combine elements of structure, nutrients, water quality, and light to create a favorable and productive environment for living things. Physically, the body of the reef provides a substrate and point of attachment for many species, especially more sedentary species groups such as crustaceans and mollusks. Even among more active species, the physical characteristics of the reef provide cavities for shelter and breeding. Upon this structure, high densities of prey species attract proportionally high densities of predators.

Reef-building corals take up dissolved calcium from seawater and accrete it to produce the reef substrate. Because the reef forms in well-lit waters, light is available in combination with calcium and other nutrients, creating a favorable environment for photosynthesis to take place. Interacting with nutrient and light availability is a generally high water quality, produced in part by abundant populations of sponges on the reef's surface. Sponges, using the reef for support, circulate and cleanse the surrounding water through their own bodies, enhancing water quality, lowering turbidity, and increasing the transparency of the water to allow penetration of light to greater depths.

Like their terrestrial counterparts, the tropical rainforests, coral reefs are, for all their beauty and diversity, fragile systems. They can be degraded or destroyed by disease, bleaching, sediment, pollution, overfishing, or direct destruction. They are today in a global state of accelerating decline, with 10% of the world's reefs now considered degraded and projections for another 30% expected to be lost in the next 20 years alone. Ten percent to 16% of coral reefs worldwide have been destroyed, and 46% of the living coral on reefs in the Indian Ocean have been killed. Coral reefs are arguably in the worst possible physical locations to avoid human impacts. Each year, as the world human population adds approximately 77 million people to its current level of 6.3 billion, most of the new individuals will be added in coastal areas of developing countries, in immediate proximity to the world's great reef systems (Hoegh-Guldberg 2004:463). But the developed world adds to reef degradation as well. As coral reefs become more popular designations for western "ecotourists," the problems of divers touching or walking on reefs, or physically breaking off pieces of coral from the reef for souvenirs becomes an increasingly serious problem, leading to the degradation of some of the world's most complex reef structures.

Of the above lists of threats, two deserve some further elaboration. ***Bleaching*** is a response that occurs in temperature-stressed corals, and it does not take much temperature increase to cause it. Studies of bleached corals reveal that water temperatures as little as 1–2°C above normal maximums, if sustained for even a few weeks, will lead to bleaching in corals (Spalding 2004). Although some recovery from bleaching is possible, "recovered" corals typically show fewer individuals, less surface area coverage on the reef, slower growth, reduced competitive ability, and greater subsequent susceptibility and mortality to other diseases. Bleaching was unknown in corals prior to the 1970s, but now is a worldwide problem (Figure 11.12). As noted in Chapter 5, current models of worldwide ocean temperature change estimate that all six of the world's major coral reef regions will exceed thresholds for coral bleaching during the period from 2030 to 2050, such that, under these projected temperature regimes, coral bleaching will become an annual event (Hoegh-Guldberg 2005).

Some coral research scientists, such as Andrew Baker, have suggested, based on transplants and other experimental manipulations of coral, that bleaching may be an adaptive response that "offers a high-risk ecological opportunity for reef corals to rid themselves rapidly of suboptimal algae and to acquire new [symbiotic algal] partners" (Baker 2001:765). Specifically, Baker transplanted (switched) shallow corals (found at depths of 2–3 m) and deep corals (found at depths of 20–23 m) in Caribbean reef building coral species and monitored their responses over 12 months.

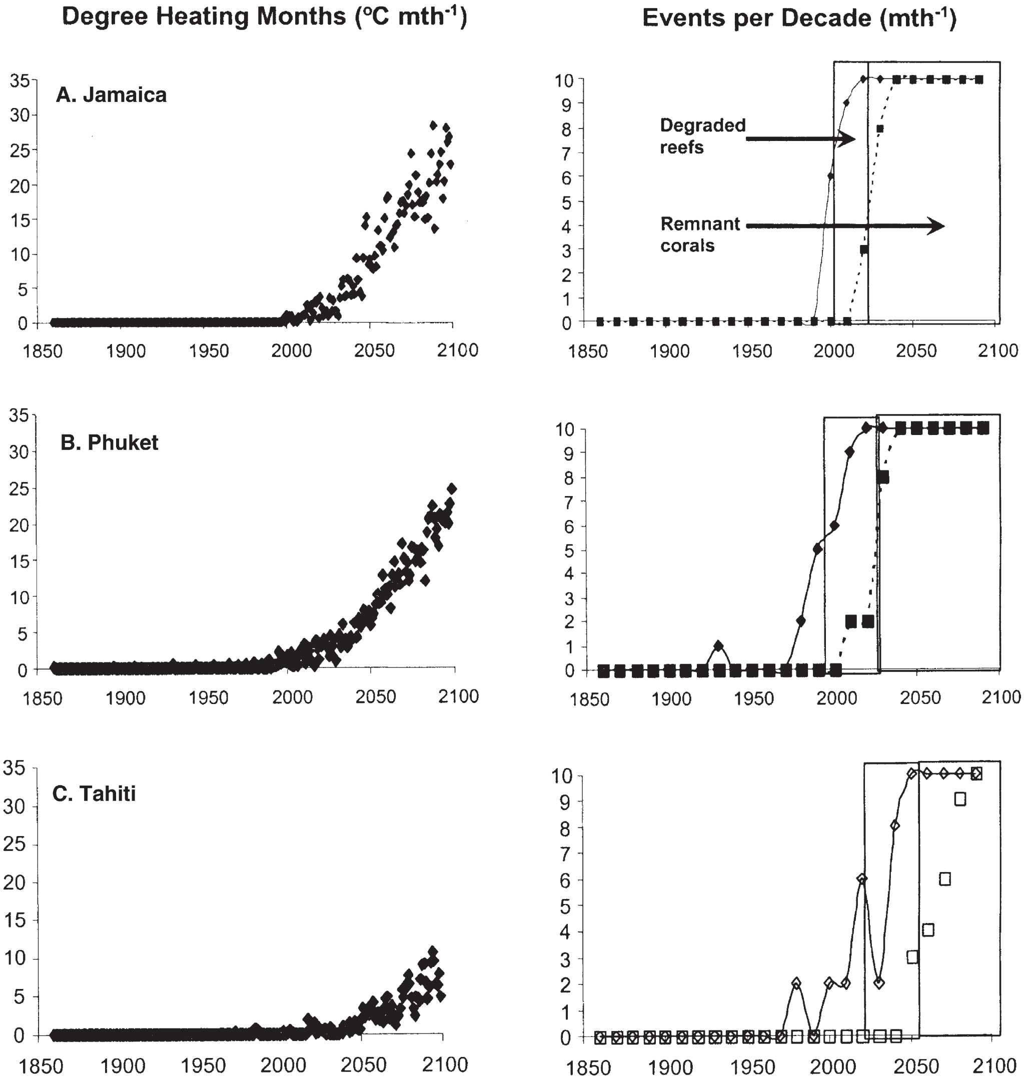


FIGURE 11.12. Patterns of bleaching projected for coral reefs along the southern coast of (A) Jamaica, (B) Phuket, and (C) Tahiti from 1860 through 2100. Sea temperature data from the ECHAM4/OPYC3 model (Roeckner et al. 1996). *Left side* shows accumulated Degree Heating Months (DHM) values once they exceeded 0.5 DHM. *Right side* shows frequency of bleaching events per decade over next century (DHM > 0.5, solid line) and severe events (DHM > 3.2, dotted line). In right side graphs, left column shows period in which corals are in decline (coral cover beginning to decrease). Right column shows period in which coral is remnant (<5% coverage of reef), based on assumption that coral communities cannot survive three or more severe bleaching events per decade, based on observations in Okinawa, Palau, Seychelles, and Scott Reef in 1998. (Hoegh-Guldberg 2004. Copyright 2004 Springer-Verlag, New York, Inc. With the kind permission of Springer Science and Business Media.)

When deep water species were moved to shallow waters, 11 of the 24 transplanted colonies showed significant bleaching, but, after 12 months, there was no mortality (none of the transplanted colonies died). In contrast, when shallow water species were transplanted to deeper water, they showed no bleaching (0 of 37 colonies bleached), but after 12 months, 7 of the 37 transplanted colonies had died. Thus, Baker proposes that coral bleaching promotes rapid response to environmental change by facilitating compensatory change in the algal symbiont communities associated with the coral, the so called "adaptive bleaching hypothesis" or ABH. In other words, bleaching, according to Baker, is a way for corals to rapidly rid themselves of poorly adapted symbionts and replace them quickly with algal species better-adapted to warmer temperatures. "This strategy," asserts Baker, "could be an advantage to coral reefs that face increasingly frequent and severe episodes of mass bleaching as a result of projected climate change" (Baker 2001:765). Many coral ecologists disagree with Baker. Hoegh-Guldberg and her colleagues at Australia's Centre for Marine Studies at the University of Queensland criticized Baker's experiments for failing to control for temperature manipulation, failing to clearly define "stresses" to which the transplanted corals were subjected, and that his molecular analysis techniques could not distinguish new symbiont algal genotypes that might have invaded bleached corals from rare genotypes that were already present in the host (Hoegh-Guldberg et al. 2002). Thus, Hoegh-Guldberg et al. concluded, “we consider that the evidence in favor of the ABH remains scant in the absence of observations that the genotypes of symbionts in corals become more thermally robust during and after mass bleaching” (Hoegh-Guldberg et al. 2002:602). Hoegh-Guldberg offered a more pessimistic assessment regarding the ability of corals to adapt to ongoing climate change. She concluded that if even the mildest changes forecast in climate models are true, “reefs will soon progress through a degraded state to one in which corals are rare, remnant organisms. Reefs will be largely devoid of reef-building corals” (Hoegh-Guldberg 2004:475).

Destruction of coral reefs also occurs through ***blast fishing***, a form of direct destruction of coral reefs in which explosives are used to harvest fish from the reef. A single blast can devastate thousands of cubic meters of coral reef, destroying not only individual fish but the structure upon which the community depends. Such fishing “technique” destroys what may have taken hundreds or thousands of years for marine organisms to build (Agardy 1997). Blast fishing, even though now outlawed by most governments, is still a common practice. But there are methods of managing, conserving, and rehabilitating “blasted” corals that can be successful on local scales.

11.4.4. Rehabilitation Techniques for Coral Reefs

Indonesia’s Komodo National Park (KNP), a group of small tropical islands in south-central Indonesia, contains some of the world’s most beautiful and diverse coral reef systems. It is also an area where reefs have been devastated by blast fishing, leaving the affected reefs as little more than a pile of rubble on the ocean floor. Coral reef restorationist Helen Fox and her colleagues at the University of California (USA) – Berkeley, working with members of The Nature Conservancy’s Coastal and Marine Program in Indonesia, have been engaged in an extended rehabilitation effort to restore such damaged systems. Worldwide, reef restoration techniques have included the transplanting of living corals from one location to another, installing branching ceramic stoneware on damaged reefs for new corals to colonize, and using electrolysis within reef-associated water currents to accelerated the deposition of calcium carbonate and enhance the growth of existing or transplanted corals. These techniques all have something in common, and it is not that they all work equally well. Rather, all are extremely expensive, labor intensive, and sometimes incur a high rate of mortality in coral transplants. Costs for restoration efforts using these techniques have ranged from US$13,000/ha to more that US$100 million/ha (Fox et al. 2005). These prices are beyond the budgets of most conservation organizations and even many government agencies, and out of the question for most countries in the developing world.

Fox et al. began with an experiment using low-cost materials. In 1 m^2 plots, they measured the colonization success of new corals on wide-mesh fishing net (~5 cm mesh) attached to rock rubble, cement slabs pinned to the rubble, and piles of rocks on top of the rubble (Fox et al. 2005). The rock stabilization plots were by far the most successful, followed by cement and netting. Not surprisingly, untreated rubble did worst (Figure 11.13).

Although this experiment was a useful first step, coral rehabilitation cannot be successful using 1 m^2 plots because, in high current areas, rock rubble piles this small will be buried or broken into pieces over time. Taking their effort to a larger scale, Fox et al. created 100 m^2 (10 × 10 m) rock rubble piles and monitored

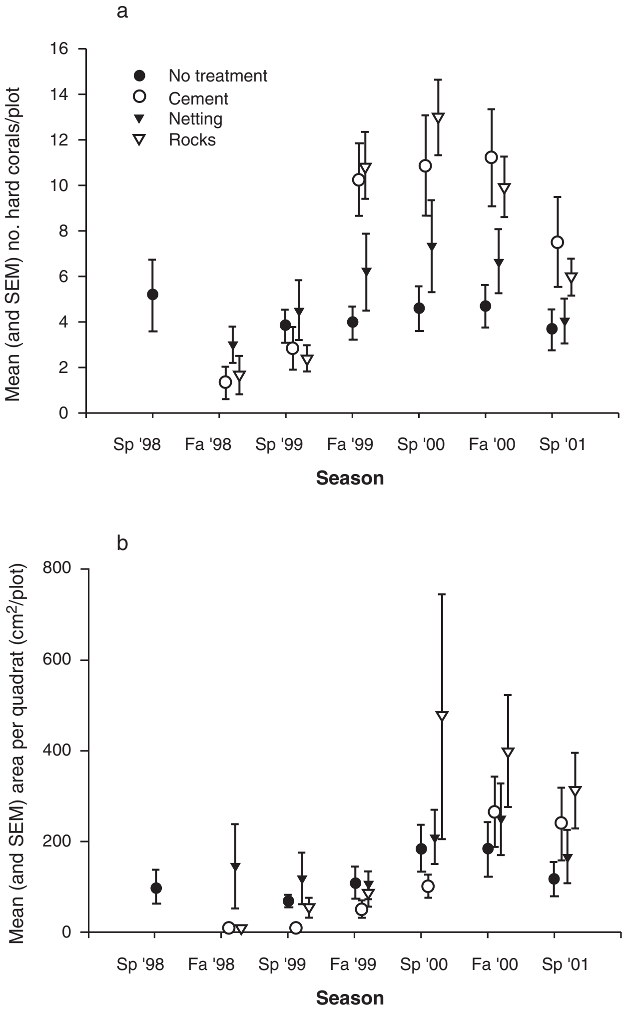


FIGURE 11.13. Recruitment and growth of corals onto 1 m^2 treatments of cement, netting, rock piles, and untreated sites on a formerly blasted coral reef in Komodo National Park, Indonesia from sp (spring) 1998 through sp 2001. (a) Mean and SE of coral recruits plot and (b) mean and SE of total area (cm^2) covered by coral recruits per plot. Fa = fall. (Fox et al., Experimental assessment of coral reef rehabilitation following blast fishing, *Conservation Biology*, Copyright 2005 by Blackwell Publishing.)

their colonization by corals. The results were encouraging. "Recruitment of hard coral and cover increased significantly in the mid-scale studies. The rock piles quickly developed a 'biofilm' and were colonized by coralline algae and other encrusting organisms" (Fox et al. 2005:102). Given the success of rock rubble piles this size, Fox et al. took their effort to a still larger scale, transforming approximately 6,430 m^2 of dead coral rubble into four highly structured designs at four different locations. On sites of this size, Fox et al. noted that "Scleractinian [hard coral] recruits quickly settled on the rock piles, with considerable recruitment of hard corals after approximately 1 year" (Fox et al. 2005:104). Overall, Fox and her colleagues demonstrated that coral recruitment could be enhanced by creating stable, spatially complex structures high enough above reef rubble to minimize burial and abrasion. Recruitment on the structured rock piles was more than 20 times higher than on untreated rubble, and there was substantial recruitment of hard corals in as little as 6 months. Although labor was required to create appropriate structure, the materials were ready at hand, available at little or no cost. "Economically," Fox et al. noted, "substrate stabilization using locally available rock compares favorably with other methods …, rehabilitation treatments in the Maldives cost from US$40 to US$160/m^2, and rehabilitation projects in the Florida Keys National Marine Sanctuary cost from US$550 to US$10,000/m^2, clearly unreasonable for large-scale rehabilitation in developing countries …" (Fox et al. 2005:105). In their study, rehabilitation costs were approximately US$5/m^2, a figure that included materials, transportation, boat rentals, and labor. Although such rehabilitation techniques hold promise for saving coral reefs at some locations, they are of little value if reserve management is ineffective at stopping destructive practices. The variety of threats to marine habitats means that there is no single strategy that can address all problems at once. However, one emerging strategy designed to address multiple threats is the concept of the Marine Reserve.

11.5. Conservation of Marine Habitat and Biodiversity – Managing the Marine Reserve

11.5.1. Management Context, Goals and Strategies in Marine Reserves

All parks and reserves face the problem of defining appropriate biological boundaries that ensure the persistence of what the park is established to preserve. However, this problem is greater in aquatic environments, particularly in marine environments, because their third dimension, the water column, is much more dynamic and more critical to the marine community than the analagous third dimension, the air column, in a terrestrial environment. Land preserves are essentially two-dimensional, defined by their length and width on the earth's surface. The air above may be a medium for flight, some passive dispersion, and essential elements and compounds in biological reactions like respiration and photosynthesis, but it is also relatively homogenous. In contrast, the water column above a seabed is far more active. In addition to plant and animal communities on the ocean floor, the water column itself contains communities of its own, perpetually drifting or swimming in and through it. Spores, eggs, and young of even the most sedentary species must use the water column for reproduction, dispersal and development (Kenchington 1990). At most times and places, most photosynthesis, respiration, and transport of matter and energy take place within this water column.

The water mass has enormous effect on issues of reserve scale. During early phases of development, most marine species have far greater dispersal distances than terrestrial species. Some continue to remain highly mobile throughout life, others become sessile as adults. Kenchington (1990) identifies four basic life history categories of marine creatures relevant to the question of spatial scale (Figure 11.14): (1) creatures with fixed or restricted movement in their adult phase with no planktonic (drifting) phase (box A); (2) creatures in which one phase is fixed and the other is planktonic or pelagic (box B); (3) creatures in which adults have large but defined territories but planktonic larvae (box C); and (4) creatures in which all phases of life are planktonic or pelagic (box D).

POINTS OF ENGAGEMENT – QUESTION 1

Make a copy of Figure 11.14. Now, with a dotted line, mark out a square within the figure, beginning at the origin of the X and Y axes, that would correspond to a 100 km^2 (10 × 10 km) marine reserve. Which category or categories of creatures are fully protected during all life history phases within this hypothetical reserve? Which are only partially protected? Which category is least protected? What are the implications?

Historically, marine conservation efforts have typically used three basic approaches, alone or in combination. These are: (1) creating priority-setting, usually area-specific management plans that direct conservation management and environmental education for targeted areas or species; (2) establishing a marine reserve in which "taking" activities are excluded; or (3) establishing marine protected areas (MPAs). MPAs usually have less restrictive regulations than marine reserves, although they are sometimes nested within them. MPAs usually restrict allowable

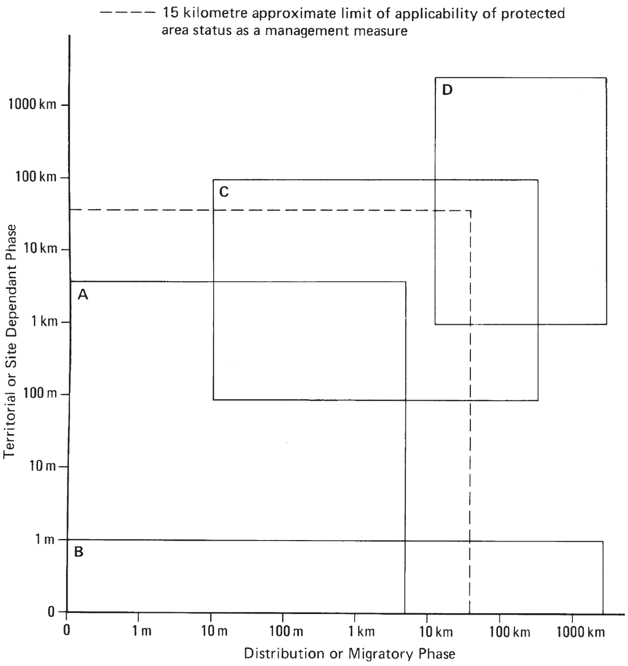


FIGURE 11.14. Four categories of life cycles characteristic of marine creatures with respect to spatial scale. Box A represents creatures with fixed or restricted movement in their adult phase with no planktonic (drifting) phase. Box B represents creatures in which one phase is fixed and the other is planktonic or pelagic. Box C represents creatures in which adults have large, defined territories but planktonic larvae. Box D represents creatures in which all phases of life are planktonic or pelagic (box D). (Kenchington, Managing marine environments, Copyright 1990 Taylor & Francis.)

catch, season of catch, catch effort, catchable species, or type of fishing effort and gear permitted for use.

Three goals that marine reserves and MPAs are designed to meet simultaneously include: (1) protecting marine and coastal biodiversity, (2) improving the productivity of local fisheries, or at least ensuring that marine productivity is not undermined by uncontrolled exploitation, and (3) focusing efforts for restoration of vital areas that may be presently degraded but have potential to support healthy marine ecosystems in the future (Agardy 1997). To these ends, marine reserves have been established worldwide with a variety of names, jurisdictions, and purposes. Within reserves, areas closed to all types of marine fishing and harvesting are often designated as ***harvest refugia*** or ***no-take zones***. These are generally designed to protect a particular commercial stock or group of stocks from overexploitation. At large scales, "biosphere reserves," administered by the United Nations' Educational, Scientific, and Cultural Organization (UNESCO), include larger marine reserves usually divided into three zones, much like their terrestrial equivalents of Multiple-Use Modules (MUMS) examined in Chapter 10. Like a MUM, there are typically "core" reserves are areas with little or no harvesting or other activities surrounded by "buffer" areas where limited harvest and other activities are permitted. Around the buffers are "transition" areas that are least protected and often administered with regulations most like those outside the reserve (Sobel 1993). At small scales, more limited reserves may be established to achieve a more limited set of conservation objectives, or even only one.

As in terrestrial conservation reserves, size is a key consideration for marine reserves. An effective marine protected area must be large enough to retain a large proportion of the mobile marine organisms within its boundaries. Migratory marine mammals, fishes, and invertebrates require larger marine protected areas. Their high rates of offshore, seasonal, and ocean-wide migrations mean that substantial portions of their lives are spent outside small, protected coastal areas. Patterns of larval accumulation and retention should be compared between potential areas being considered for reserve status because both behavior and oceanographic processes limit dispersal distance. Therefore, relatively small spatial errors in the placement of a marine reserve or network of marine reserves can mean the difference between successful dispersal and gene flow for many species of planktonic invertebrates and a state of isolation and eventual extinction. For marine reserves generally, theoretical models suggest a minimum size of at least twice the median dispersal distance for an isolated marine protection area to sustain viable populations. As more marine protected areas are included in a network design, the minimum size decreases because other protected locations are within dispersal distances to provide propagules to sustain the local population.

Efforts to establish marine reserves have varied in effectiveness according to region and country. There are 135 legally protected marine and coastal areas in the Greater Caribbean Basin alone (Dixon et al. 1995); France has five fully operational reserves; Spain has designated 21; and Italy has established 16, of which three are now operational. The United States has 12 designated marine sanctuaries, administered under the National Marine Sanctuary Program (NMSP) and officially known as National Oceanic and Atmospheric Administration (NOAA) Marine Sanctuaries. The NMSP is a kind of marine equivalent to the US National Park Service, in that it includes preservation of marine sites of historical and culturally significance, as well as other designated sites that were not necessarily chosen to conserve natural ecosystems or biodiversity. The US marine sanctuaries are not true "marine reserves" according to strict international definitions, and the US marine sanctuary program has been criticized because its "sanctuaries" are considered too small (less than 1% of US territorial waters) and unprotected (less than 0.1% are no-take areas) (Agardy 1999). But the US has established large marine reserves off the Florida Keys and the central California coast, and the NMSP has demonstrated a strong commitment to seeing the reserves persist and to receive effective protection. Within this variety of management goals, strategies and national efforts, we can examine specific cases of individual marine reserves and their management approaches to better understand their role in conservation.

11.5.2. Tourist-Recreation Marine Reserves: The Bonaire Marine Park

Marine reserves are not the exclusive domain of large nations. The tiny Netherlands Antilles off the coast of Venezuela established the Bonaire Marine Park (BMP) around the island of Bonaire in 1979. BMP is neither a vast, multiple-use area nor a strictly no-take, closed marine reserve for scientific research and conservation. It belongs to a category that could be called the "tourist-recreation reserve."

BMP was established primarily to preserve the aesthetic beauty of local marine resources for the enjoyment of snorkel and scuba divers, a mainstay of the island's tourist-driven economy (Dixon et al. 1995). Approximately 38.000 people visit Bonaire Marine Park each year, of which about 28,000 actually use the marine environment as swimmers, divers, and fishers, and the number of visitors has been increasing at the rate of 9–10% annually. To accommodate divers within the marine park, Bonaire established a "snorkel trail" as well as a series of free-standing platforms throughout the reef area. Studies of the park show that tourism and conservation are interactive joint products of the marine park, but that use levels by tourists cannot increase indefinitely, even in a relatively "non-consumptive" activity like diving. A "threshold" level exists in the park for diving pressure on reefs. Underwater areas around platforms that receive 4,000–6,000 dives per year begin to show signs of stress and wear, and coral cover and species diversity both begin to decline at this point (Dixon et al. 1995). However, the distribution of funds from diving creates an environment that produces pressure to increase the number of divers. For most divers, diving at Bonaire is part of a pre-paid travel package previously arranged with agents in the US and Europe. As part of the arrangement, the diver receives "vouchers" that cover most other expenses such as lodging, transportation, and food. Divers who come under these conditions often spend very little additional money. Local residents are reimbursed for a portion of the vouchers by sending them back to the US or European agents, but only after large commissions are deducted. As a result, income to locals from diver visitation may be marginal, and the economic benefit of each additional diver that can be added to total annual visitation is relatively large. However, if increasing stress leads to a loss of world-class diving experiences at Bonaire, fewer visitors will come and total income will decline. Assuming that diving will continue at least at its present rate (the local economy has few other sources of income beyond subsistence agriculture and fishing), current suggestions to maintain the quality of the marine park include better distribution of divers, better diver education and training in "diver etiquette," and better regulation of underwater activities. However, as Dixon et al. (1995) noted, "These management measures do not *increase* the tolerance of marine systems to stress, rather they help to distribute the burden more evenly across the ecosystem. Such measures require both money and legal authority." Greater legal authority to protect reefs is possible, but local citizens have been reluctant to grant the park more regulatory authority than it already has to regulate diving operators and cruise boats in the park, practices through which many local citizens make their living (Dixon et al. 1995).

The Bonaire Marine Park illustrates the threats that tourism poses to coral reefs described earlier, as well as the dilemma of conflating values and purposes that was addressed in Chapter 2. If the real value of the marine resources is viewed as economic rather than intrinsic, then the resources themselves may be degraded even as economic revenues rise from charges for seeing and photographing these resources. It is possible that such degradation might have no adverse economic effects because divers would gradually become accustomed to decreasing quality of diving experience. Some marine conservationists have advocated that tourism and recreation should become the primary uses of the marine environment, the basis for appreciation and enjoyment of marine environments, and the foundation of long-term social and economic benefits for the local, national, and global community (Kenchington 1990). The experience of the Bonaire Marine Park shows that this optimism is premature. Tourism can have a destructive effect on marine populations and habitats, and recreational use that is not well planned will lead to degradation of valued resources, conflicts between conservation values and economic interests, and little benefit to individuals in the local economy. In contrast, properly planned ecotourism can move beyond conflict, and even coexistence, to a symbiotic relationship in which local citizens take responsibility for the resource, marketing opportunities to enjoy the resource in profitable but non-destructive ways (Kenchington 1990). But in order for this to happen, practical management steps must be taken: (1) use of the resource, even if non-consumptive, must be restricted to a level that the resource can sustainably support; (2) users must be dispersed to avoid concentrations of use that could be destructive to the resource; and (3) where possible, resource sites must be "hardened" by facilities and structures that allow sites to bear use without degradation. All of these issues are now being dealt with at BMP through the development of a comprehensive management plan, which includes provision for standardized diver training, prohibitions against harming marine creatures or coral reefs, and the establishment of standardized monitoring protocols to protect the park's natural resources (http://www.bmp.org/management.html).

11.5.3. Protection at Ecosystem Levels: Australia's Great Barrier Reef Marine Park

One of the best examples of a large marine reserve managed comprehensively as a functional ecosystem is Australia's

Great Barrier Reef Marine Park (GBRMP), one of the world's premier protected areas, and part of the Biosphere Reserve and World Heritage Site programs. The Great Barrier Reef itself is a vast complex of some 2,900 individual reefs and 250 cays (low islands or reefs made of sand or coral) stretching along the continental shelf of northeast Australia from just south of the Tropic of Capricorn to the Torres Strait. The system possesses 71 genera of coral alone. The Great Barrier Reef was relatively inaccessible to humans until the 1960s. The GBRMP that attempts to preserve it is in many ways exceptional among marine preserves. The preserve was not established to stop or solve an existing problem or degradation of the reef, but was formed in anticipation of future problems that were just beginning to emerge. In 1967, a private Australian firm filed an application for permission to take coral limestone from a part of the reef for use in the production of agricultural lime. The Wildlife Preservation Society of Australia perceived this application as the first step in setting a precedent for dangerous and destructive processes that could eventually destroy the reef. With other conservation groups joining the lead of The Wildlife Preservation Society, public outcry led to the refusal of the permit application by the provincial government (Queensland). Further controversies over offshore oil drilling in the reef area and outbreaks of the crown-of-thorns starfish (*Acanthaster planci*), which destroyed reef corals, led to legislation that established the GBRMP (Kenchington 1990).

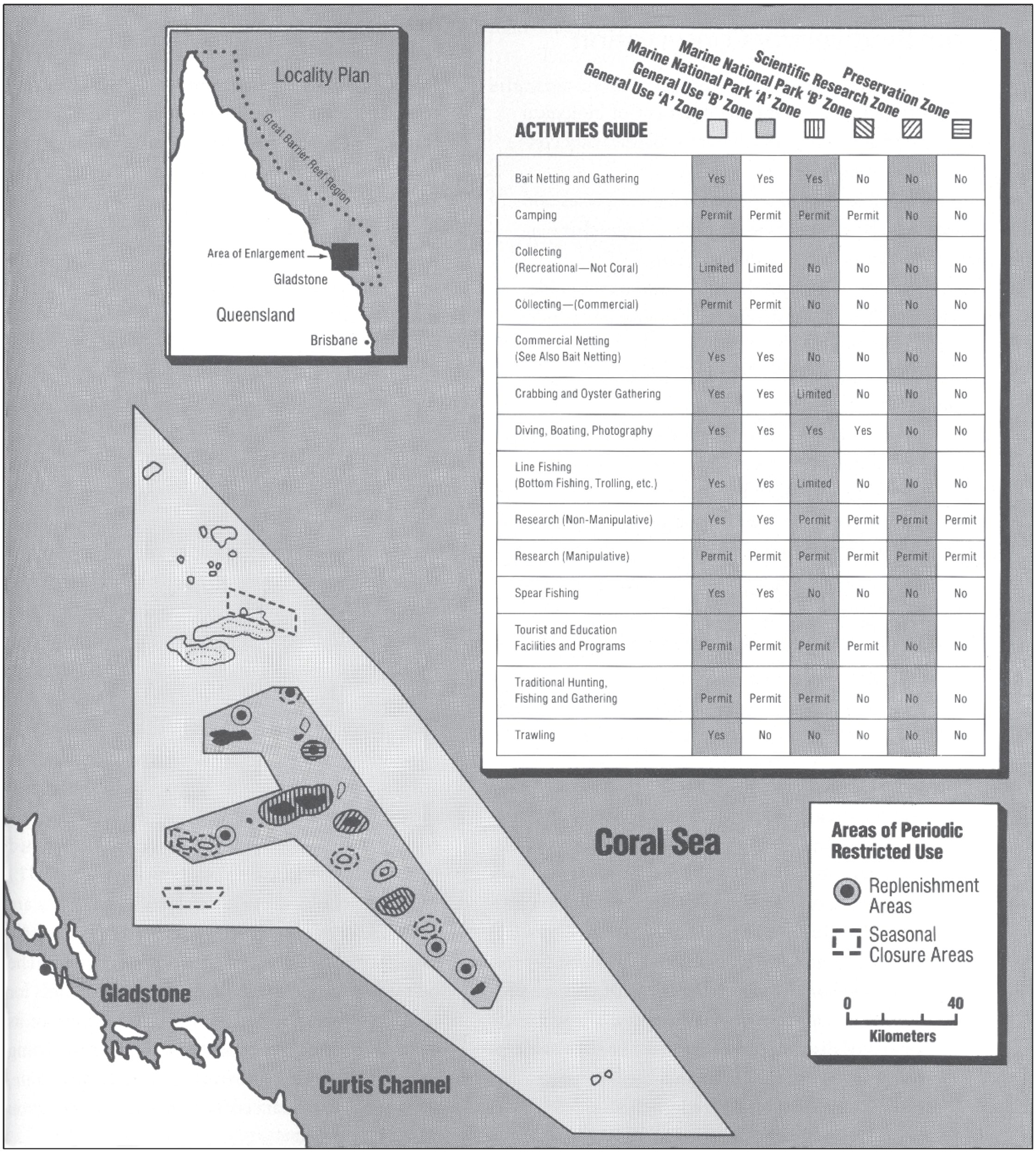
Today the GBMRP is a vast multiple-use area managed by establishing different zones within the park for different uses, through which it has successfully accommodated a variety of user groups (Agardy 1999; Figure 11.15). Much of its success is attributable to careful attention to the criteria earlier described for successful marine reserves. Rigorous scientific study has helped to define park boundaries and management policies, but the key to its success has been widespread stakeholder involvement through an extensive participatory network which has incorporated not only scientific data, but socioeconomic, political, and cultural objectives into the park's management, building a broad base of support for its conservation objectives. However, even in this exemplary park there are serious problems. For all its size and jurisdictional power, the GBRMP Authority that manages the park has no control over land-based inputs that pose significant threats to its coral reefs, commercial fish stocks, and endangered species. Its jurisdiction stops at the shoreline, and it is powerless to stop influxes of sediments and chemical pollutants that pour into its system (Agardy 1999).

11.5.4. The "Co-Management" Model – Shared Authority Between Local Citizens and Government Agencies

Although Bonaire and Great Barrier Reef protect systems of vastly different scales with different objectives, both are administered through government agencies which assume the primary responsibility for the integrity of the reserve and its conservation goals. In recent years, an alternative model has emerged in marine and other kinds of conservation reserves, a model known as ***co-management***.

Co-management is a conservation strategy that attempts to simultaneously address biological, cultural, economic, and political concerns through collaboration and integration in conservation efforts between local communities and government authorities. It can be an effective strategy, and sometimes the only viable approach, in countries where governments have limited resources and insufficient capacity for enforcement of environmental laws. In a typical co-management system, government agency personnel, such as park administrators, share responsibility and decision-making power with local residents, usually through the mechanism of a "council" or equivalent structure that includes representatives of the agency and local stakeholders who represent various interest groups. In addition to participation in the council and its decision-making functions, local residents also perform services in education, research, ecological monitoring, or law enforcement within the park. In so doing, managerial expertise that is typically the domain of government employees is complemented by traditional knowledge of the area and its natural community possessed by local citizens. But could such a system work in a real marine reserve, and what would it look like if it did?

The ecosystems of the Comoros Islands in the West Indian Ocean, a biodiversity hotspot with high endemism and diverse tropical marine environments, are adversely affected by existing ecological, socioeconomic, and political conditions. Most local residents are poor, and many make a living in whole or in part by harvesting marine resources from the system, including the system "protected" within the park. The government of the Comoros, like its citizens, is not wealthy, and its resources to enforce park protection are limited. So are its educational and professional expertise, endowing it with only limited scientific knowledge of the park's marine systems and species. Despite these limitations, the Comoros Government, with help from the World Conservation Union (IUCN) and funding from the World Bank's Global Environmental Facility (GEF) and the United Nations Development Programme (UNDP) established Mohéli Marine Park in the Federal Islamic Republic of the Comoros. The goals of the park were to stop the loss of biodiversity in the Comoros while at the same time developing increased local capacity for and participation in natural resource management. The Mohéli Marine Park contains both core reserve (no take) areas as well as protected areas within the park which permit marine harvests according to prescribed methods and limits (Figure 11.16). The park contains a diverse environment of coastal mangroves, seagrass beds, inshore and offshore coral reefs, and its beach areas include some of the world's best nesting beaches for green turtles, where up to 5,000 females come ashore each year to build nests and lay their eggs (Granek and Brown 2005).



ACTIVITIES GUIDE

	General Use 'A' Zone	General Use 'B' Zone	Marine National Park 'A' Zone	Marine National Park 'B' Zone	Scientific Research Zone	Preservation Zone
Bait Netting and Gathering	Yes	Yes	Yes	No	No	No
Camping	Permit	Permit	Permit	Permit	No	No
Collecting (Recreational—Not Coral)	Limited	Limited	No	No	No	No
Collecting—(Commercial)	Permit	Permit	No	No	No	No
Commercial Netting (See Also Bait Netting)	Yes	Yes	No	No	No	No
Crabbing and Oyster Gathering	Yes	Yes	Limited	No	No	No
Diving, Boating, Photography	Yes	Yes	Yes	Yes	No	No
Line Fishing (Bottom Fishing, Trolling, etc.)	Yes	Yes	Limited	No	No	No
Research (Non-Manipulative)	Yes	Yes	Permit	Permit	Permit	Permit
Research (Manipulative)	Permit	Permit	Permit	Permit	Permit	Permit
Spear Fishing	Yes	Yes	No	No	No	No
Tourist and Education Facilities and Programs	Permit	Permit	Permit	Permit	No	No
Traditional Hunting, Fishing and Gathering	Permit	Permit	Permit	No	No	No
Trawling	Yes	No	No	No	No	No

FIGURE 11.15. Management zones in the Capricornia section of the Great Barrier Reef Marine Park, Australia. (Copyright 1992 World Resources Institute, Washington, DC. Used by permission.)

Faced with the daunting task of protecting and managing the park with limited resources and capacities, the Comoros government, with the help of IUCN, GEF, and UNDP, developed a co-management strategy requiring participation from both government and local community organizations. At the local level, this specifically required participation from village environmental organizations, known in the Comoros as *Ulanga*, the Comorian name for the environment, as well as local village fishers' associations, which included individuals with high levels of concern for the state of biotic resources in the park, resources which had traditionally supported their livelihood. Overall program goals were to protect Comorian biodiversity and improve local and regional fisheries. The plan required representation of the local community in the process of conservation management, scientific monitoring, and environmental education. To accomplish this, village residents nominated representatives to serve as "ecoguards." The ecoguards would be responsible for monitoring local marine resources, enforcing park regulations, and representing the interests of the community to the government. Ecoguards were selected based on their perceived commitment to conservation, previous involvement in *Ulanga* or

FIGURE 11.16. Map of Mohéli Marine Park in the Comoros Archipelago consisting of ten core "no-take" reserves (shaded areas) existing within a larger park area of regulated harvesting. (Granek and Brown. Co-management approach to marine conservation in Mohéli, Comoros Islands, *Conservation Biology*. Copyright 2005 by Blackwell Publishing.)

related activities, respect and trust of village members, their ability to help foster community participation in park programs, and the level of confidence of fellow villagers in their ability to patrol their zone of the park, enforce park regulations, and educate park visitors (Granek and Brown 2005).

Once elected, the ecoguards in Mohéli performed admirably. They improved communication and cooperation among local villages that had a long history of conflict with one another over resource use. They developed novel and widely embraced educational programs for local school children, including a special environmental magazine, *Mwana wa Nyamba* (*The Baby Turtle*) and a special "field day," *Journée de la Tortue* ("Day of the Turtle"), that permitted school children to observe female turtles making nests and laying eggs on local beaches. Over several years, Mohéli integrated education, local knowledge, and community commitment into a viable conservation program that overcame limited financial resources, weak government enforcement capacities, and limited scientific data. The co-management approach empowered community leaders and circumvented political structures in the government that would have excluded them. It inspired local interest in tracking the park's success, leading to greater participation in monitoring park resources. In recognition of these achievements, Mohéli Park received the UNDP Equator Initiative Award, presented at the World Summit on Sustainable Development in 2002, with a prize of US$30,000 to further develop the park's programs and infrastructure (Granek and Brown 2005).

The Mohéli program was, by many standards, a success, but it also had shortcomings. Park design was based on limited scientific data which impeded ability to accomplish conservation goals. Despite the admirable performance of the ecoguards, inadequate governmental resources for policing the park worked against preserving its biodiversity. Many violators were not arrested. Those that were often were released by government officials with no more than a warning. And despite commendable local initiative, regional and global issues such as overpopulation and climate change could destroy achievements produced by local effort. Current conservation initiatives rely heavily on tourism for funding, as in Bonaire, and if the current level of tourism revenue should prove insufficient, alternative funding must be found. Like Bonaire, if more tourists come to the park, its biodiversity and coral reefs could be degraded. As conservation policy experts Elise Granek and Mark Brown note, "Co-management is not a panacea for incomplete scientific data and broader economic and political problems, but it offers a potential alternative in situations faced with limited resources for addressing biodiversity conservation and natural resource loss" (Granek and Brown 2005:1731).

11.5.5. Marine Protected Areas and Commercial Fisheries

In 1982, most nations of the world adopted the conventions established at the United Nations Third Conference on the Law of the Sea (UNCLOS III). The most radical change in international law that emerged from this convention was the extension of national jurisdiction over territorial waters from the historic 12-nautical-mile standard to 200 nautical miles, a move estimated to place 90% of marine fishery resources within the jurisdiction of individual nations (Lauck et al. 1998). These enlarged areas of national jurisdiction, or exclusive economic zones (EEZs) encompassed almost 95% of the annual global yields of usable marine biomass (Tang 2003) and were seen as the saviors of international marine fishing. With this change in international law, it was optimistically believed that commercial fishing stocks would avoid becoming an example of Hardin's "tragedy of the commons" (Hardin 1968) because, with fishing and property rights more clearly defined, individual nations would be both motivated and empowered to protect marine resources now solely within their jurisdiction.

These happy, hopeful visions have yet to come true. Despite the extension of territorial limits to 200 nautical miles and more exclusive use of fisheries stocks by individual nations, commercial fisheries have collapsed all over the world. Lauck et al. (1998) argue that the answer to the problem of sustainable commercial fisheries may be the marine reserve. Far from being simply a means to enhance tourism or to preserve unique ecosystems or rare species, they assert that marine reserves should become the foundation of a new form of fisheries management that is based on a radical change of perspective. Namely, they argue we should abandon the concept that every available commercial fish stock should be exploited optimally and replace it with the strategy of "bet hedging." That is, one should assume that high levels of uncertainty are a permanent and persistent dimension of estimating the size of fish populations and their future trends. If high uncertainty is taken as a given, the optimal strategy is not to attempt to harvest a population optimally wherever it occurs, but to harvest *some* of the populations at the predicted (but uncertain) optimal level and leave a large portion unharvested as a protection against unforeseen (and uncontrollable) declines in the harvested stock.

Lauck et al. manifest their ideas in a model whose goal is to retain a fish population at more than 60% of carrying capacity. Through a series of equations that permit estimation of the proportion of the population available for harvest outside a closed area, Lauck et al. estimated the probability that the population could persist for the specified periods and levels. They assumed that half of the available population outside the reserve was captured annually, but with coefficients of variation (CV, the measure of uncertainty about the mean) assigned at six different levels from 18% to 61%, and they varied the fraction of total area available for harvesting (Lauck et al.1998).

The effect of catch variation and variation in exploitation rates had dramatic effects in this model. Even with a moderate amount of variation in the catch (CV < 50%), the probability of the population persisting for 20 years dropped drastically when the amount of exploitable area became greater than 30% (Figure 11.17). If the catch percentage was more variable, the probability of the population's persistence was less than one (not certain) even if only 5% of the area was harvested. The probability of successfully protecting the fish stock increased if the harvest was reduced to lower levels, and at lower levels, more of the total area could be made available to fishing. Two conclusions emerged from the model. First, "a reserve can simultaneously lead to stock protection and a higher level of catch," and "it is possible to maximize catch while protecting the stock" (Lauck et al. 1998:S77). Thus, Lauck et al. reach the radical but rational conclusion that marine protected areas provide the "best approach to implementing the precautionary principle and achieving sustainability in marine fisheries" (Lauck et al. 1998:S77).

Empirical data from marine reserves supports their value in restoring fish populations. Russ and Alcala (1996) compared density and biomass of large predatory fish at two small marine reserves in the Philippines with two similar control sites. They found that the longer the reserve was protected from fishing, the greater the increase in density and biomass of large predatory fish (Figure 11.18). But they also noted that unregulated fishing within the reserves, even for a short time, eliminated gains in biomass and density that had taken years to achieve. Russ and Alcala concluded that "… manage-

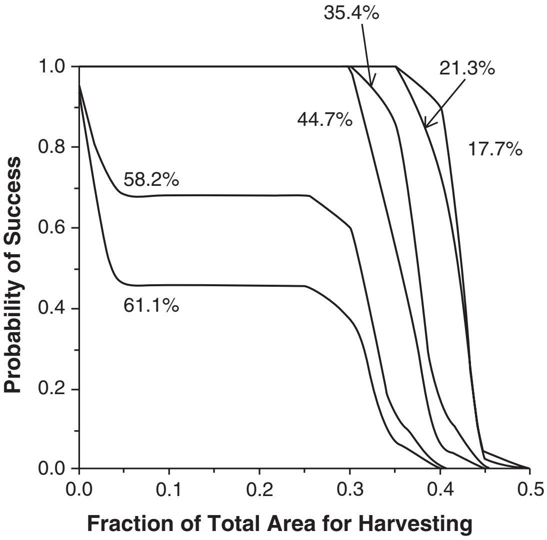


FIGURE 11.17. The probability that a fish stock remains at a size greater than 60% of its carrying capacity for 20 years depends on the fraction of area available for harvesting. When the total area for harvesting increases beyond 30%, the probability for maintaining a population size that is >0.6K (K = carrying capacity) drops rapidly. Each line represents a different value for coefficient of variation associated with the average harvest (CV is defined as the standard deviation of the harvest fraction/mean of the harvest fraction). (Lauck et al. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications* 8:S72–S78. Reprinted by permission of the Ecological Society of America.)

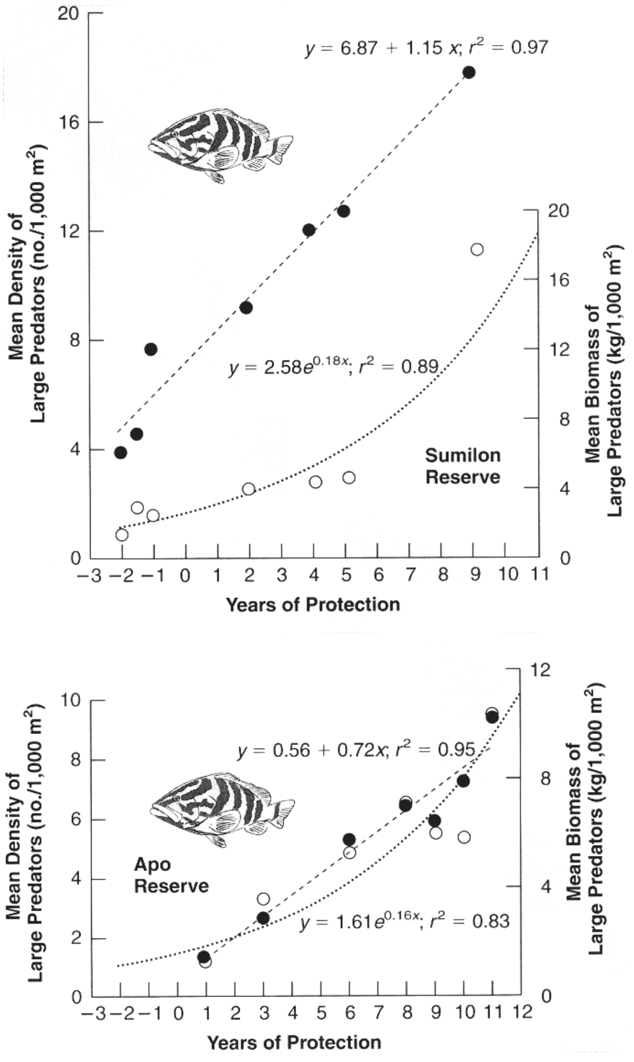


FIGURE 11.18. Changes in density (solid circles, dashed lines) and biomass (open circles, dotted lines) of large predatory fish at two small marine reserves in the Philippines with two similar control sites. The longer the reserve was protected from fishing, the greater the increase in density and biomass of large predatory species. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Adapted from Russ and Alcala. Marine reserves: rates and patterns for recovery and decline of large predatory fish. *Ecological Applications* 6:947–967. Reproduced with permission of the McGraw-Hill Companies and The Ecological Society of America.)

ment measures used to implement and maintain marine reserves must be robust in the long term, i.e., on scales of decades," (Russ and Alcala 1996:958).

POINTS OF ENGAGEMENT – QUESTION 2

Examine the data in the two graphs of Figure 11.19. Do the data support the assertion that marine reserves lead to increased populations of fish?

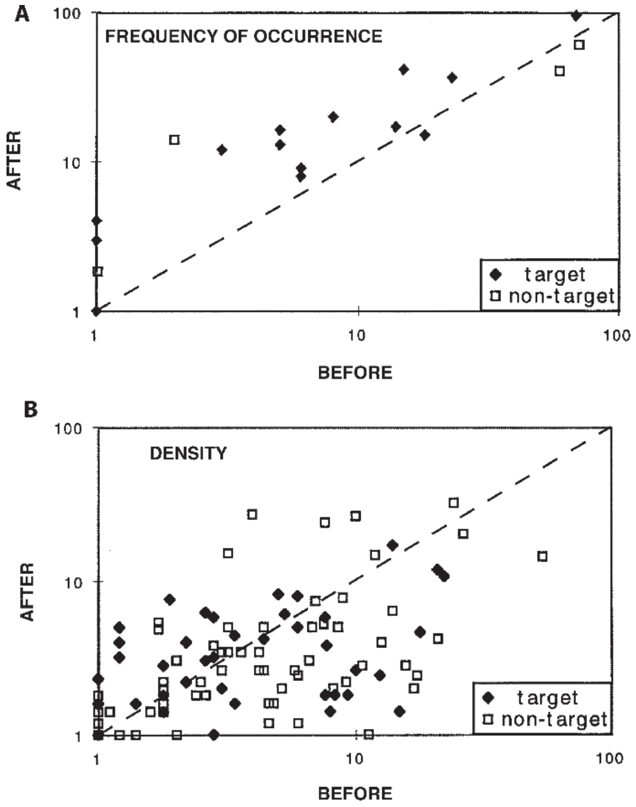


FIGURE 11.19. Frequency of occurrence (A) and density (B) of commercially targeted (solid circles) and non-targeted (open circles) fish species before and after the establishment of marine reserves. Symbols above the diagonal lines indicate species that were more frequent or had higher densities after reserve establishment. (Ruckelshaus and Hays 1998. Copyright 1998 Springer-Verlag, New York, Inc. With the kind permission of Springer Science and Business Media.)

11.5.6. Mariculture – The Case History of the Giant Clam

Not all marine areas will be placed in marine reserves. Most marine populations will continue to be exploited in open seas. An alternative strategy to stop overexploitation is ***mariculture***, the intensive commercial cultivation of certain species in limited areas. Some forms of mariculture, such as the pearl industry and oyster farming, have been practiced for centuries. Others are recent developments. However, given an ever-accelerating human demand for marine creatures as food and for other products such as jewelry or decoration, it is certain that maricultural techniques will increase in size, scope, and diversity in the next decade. Like intensive agriculture in terrestrial landscapes, mariculture concentrates disturbance of the environment; increases, intensifies, and concentrates pollution; and reduces systems to the lowest possible levels of species diversity and ecological complexity, effectively eliminating most ecosystem services. Like intensive terrestrial agriculture, however, mariculture can also provide large yields of food and other products from the creatures subjected to its management on a per area, per effort basis. Because mariculture can be so effective and efficient, it can reduce the need to disturb or exploit natural systems and their populations, which may not be resilient to disturbance or exploitation even at very low levels. The case history of the giant clam illustrates the potential value of mariculture.

Giant clams (*Tridacna* spp. and *Hippopus* spp.) include nine species of marine clams that live in shallow tropical and subtropical waters, often on coral reefs, in the Indo-Pacific, primarily in the Indo-Malay region (Figure 11.20; Lucas 1997). Only one species, *Tridacna gigas*, could truly be called “giant,” having a maximum shell length of 137 cm and a mass of about 500 kg (Lucas 1994). Other species range from 15 to 50 cm in length and average about 15 kg in weight. Nevertheless, one adult of even the smallest species would amply fill the average dinner plate, and a high demand for giant clams as food leads many to wind up there. The giant clams are limited to shallow waters because, like most corals, they live in a symbiotic relationship with microalgae known as zooxanthellae. The zooxanthellae, which are photosynthetic, use the clam’s mantle as a point of attachment, and transfer some of the organic products of photosynthesis to their clam hosts. The clam fulfills its part of the symbiosis not only by acting as the substrate for the algae, but also by providing inorganic nutrients to the zooxanthellae and exposing them to sunlight in the shallow waters. The relationship can be considered essential for both organisms, as the clam obtains much of its nutrition from these algae (Lucas 1997).

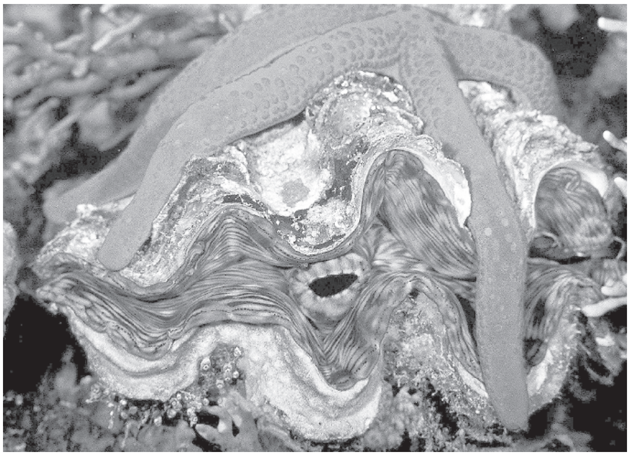


FIGURE 11.20. The giant clam (*Tridacna gigas*) (with a giant sea star attached), an endangered species that has responded favorably to intensive mariculture. (Photo by Tom Depner. Depner 2007. http://cs.brown.edu/~twd/fish/start.htm)

Because of their large size, their high value as food, and their accessibility in shallow waters, giant clams have been heavily exploited. This has led to a ban on international trade in clam products, bans on fishing for giant clams in marine reserves, limits on effort and harvestable size of clams outside of reserves, aggregation of remaining populations to facilitate reproduction, and replenishment of wild stocks with cultured clams. It is these “cultured clams” that deserve a more detailed examination.

After fertilization, the planktonic clam eggs are dispersed passively by ocean currents. Upon hatching, the clams develop into free-swimming trochophores, which, in turn, develop into small, filter-feeding, bivalved larvae called ***veligers***. After increasing in size and developing a prominent foot, the veligers settle out of the current onto a reef surface, where they will grow and metamorphose. Although the clam may move slightly after settling, where it settles is likely to be its habitat for life.

Clam mariculture makes use of this life history strategy by collecting eggs from wild clams or, more often, using eggs of existing domestic stock, and maintaining the hatching, larval, and juvenile stages in outdoor tanks. Juveniles at larger stages are moved into protective containers in the ocean, and larger individuals are later cultured without protection in the open sea (Figure 11.21). The mariculture of giant clams has no deleterious environmental effects. Even the feces produced by clams are so packed with algae (recall the clam’s symbiotic relationship with the zooxanthellae) that they are rapidly consumed by plankton-feeding fishes that reside around the clam colonies.

The mariculture of giant clams offers an environmentally friendly way to gain valuable resources from a fragile environment, the coral reef, while at the same time providing the means to supplement wild populations of clams with individuals raised in captivity. However, even this apparent success story cannot be accepted uncritically. Like sea turtle farming (Chapter 2, Ehrenfeld 1992), the mariculture of giant clams has drawbacks, some of which are the fruits of its own success. If effective, the increased supply of giant clams from mariculture could fuel increased demand for giant clams as food and ornaments, and encourage mariculture operators to remove additional quantities of eggs and adult clams from wild populations. In a climate of higher demand, pressure will increase to take clams directly from wild stocks. Consumers would not know the difference, and wild clams could be harvested with only a fraction of the time and effort needed to raise clams by mariculture. Poaching would become attractive, especially to individuals in the local culture who possess the skill to collect giant clams on their own. This last objection has been addressed, in part, through development of a village-based, clam farming program established in the Solomon Islands by the International Centre for Living Aquatic Resources Management Coastal Aquaculture Centre (Lucas 1997). Here local villagers own and work

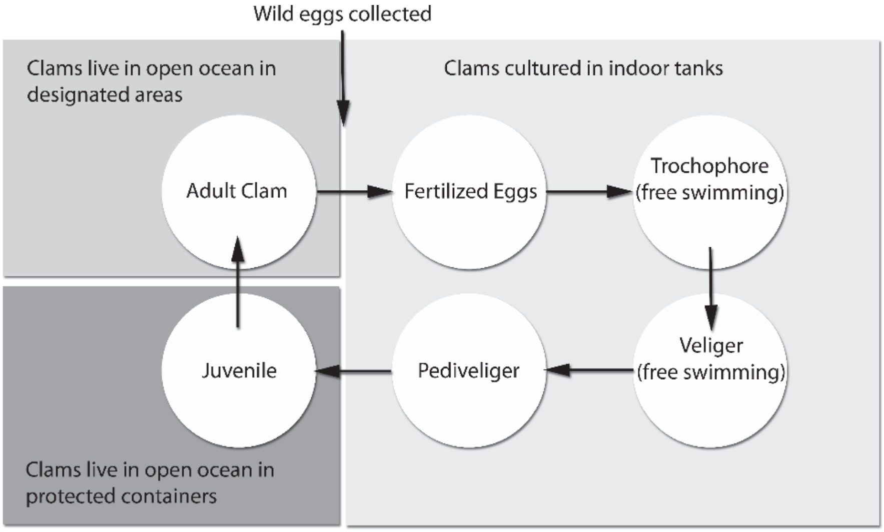


FIGURE 11.21. The life cycle of the giant clam (*Tridacna gigas*). (Original diagram designed by M. J. Bigelow.)

in all stages of the program, receiving profits and sharing risks directly, and thus also sharing incentive not to take clams from wild populations. However, not every area where clam mariculture is practiced can expect to gain this degree of local ownership. In those cases, the potential for poaching could be high.

11.5.7. Multiple and Conflicting Jurisdictions Over Marine Resources

Lamenting the current state of marine environmental law and policy, W. M. von Zharen of the Texas Institute of Oceanography wrote, "the present management of the marine ecosystem is based on a series of regimes that are directed at the various parts rather than the whole and that are, as such, ineffectual" (von Zharen 1999). Marine conservationist Elliot Norse agreed, noting that a successful marine conservation strategy must be "cross-sectoral, embracing all categories of marine ecosystems and species, all types of human use, and all sources of threats" (Norse 1993:281). As we have already explored in our discussion of law and policy (Chapter 3), international and national laws, and their respective interests, are often at odds in the conservation of marine resources. National jurisdictions over territorial waters do not always coincide with the distributions and movements of commercial fish populations, leaving these stocks vulnerable to depletion by international harvesting. Inputs of pollution from one country may flow into the territorial waters of another country. The discharge of ballast water from foreign ships into estuaries, bays, and coastal waters of another may transfer non-indigenous species that destroy local stocks of valuable native marine creatures. These problems cannot be solved without international cooperation and enforced international conservation law.

The primary documents that serve as sources for an international conservation strategy are *Agenda 21* (United Nations 1992), the *Global Biodiversity Strategy* (World Resources Institute et al. 1992), and *Caring for the Earth: Strategy for Sustainable Living* (IUCN et al. 1991). Although these documents differ in details, they agree that international strategies should aim at reducing population growth and the consumption and wasteful use of marine resources; development of an open, nondiscriminatory, equitable and environmentally sound international, multilateral trading system; and ratification of major UN documents establishing regional and global laws, policies, protocols, and organizations for marine ecosystem management, especially ratification of the third United Nations Convention on the Law Of the Sea (UNCLOS III) (Norse 1993).

One attempt to develop more consistent patterns of international cooperation has been the work of the International Organization for Standardization (ISO), which developed out of the 1992 Earth Summit meetings (von Zharen 1999). The ISO has played a leading role in developing international and regional environmental management standards that attempt to establish consistent, internationally accepted protocols in dealing with resource use and pollution in marine environments. Core principles of the ISO include a commitment to environmental management as an organizational priority; identification of appropriate legislative and regulatory requirements; identification of the environmental aspects of an organization's activities, products and services; development of management processes for achieving objectives and targets; appropriate financial and human resources to achieve targets; assignment of clear procedures for accountability; establishment of a maintenance review and audit process; and development and maintenance of communication with interested parties (von Zharen 1999).

Management actions differ in local context, but overall global strategies for protecting marine ecosystems endorsed by the World Resources Institute, the International Union for the Conservation of Nature, the United Nations Environmental Programme, and other international conservation organizations focus on three things:

1. Establishing a Commission on Ecosystem Restoration to provide technical guidance and funding for nations seeking to restore sustainability of coastal and freshwaters
2. Map, using GIS technology, macroscopic structure-forming species including coral, oyster and worm reefs, kelp and seagrass beds, and mangrove forests that provide habitat to other species
3. Develop a marine biogeographic scheme based on patterns of species endemism that can be used to establish a global system of marine protected and special management areas and use this scheme to establish a global network of marine parks (Norse 1993).

11.6. Synthesis

We know too little about aquatic habitats, especially marine habitats that cover 71% of the earth's surface and more than 90% of its livable volume. Yet we make extensive withdrawals from these poorly understood systems. The greater problem is not that we know too little, but that we may know too late. Degradation and destruction of aquatic habitats are problems of unmanaged inputs and unconstrained exploitation. To restore aquatic habitats, we must control what we put in and reduce what we take out. Future conservation of aquatic habitat will require (1) control of inputs to aquatic systems through management of surrounding land-use practices; (2) establishment of well defined, and properly enforced aquatic reserve systems consisting of lakes, rivers, and marine areas that preserve high levels of the global biodiversity of aquatic communities; (3) persistent, comprehensive research to understand aquatic systems, unfamiliar worlds in which we do not live and which, without great effort, we cannot observe; (4) reduction of our use of aquatic resources if we are to see their sustainable use continue for future generations; and (5) international cooperation, jurisdiction and ownership of the problems of marine environments. If conservation biologists do these things well, a whole new world of biodiversity awaits the next generation of scientists who dedicate their efforts to the study of these systems.

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12

Ecosystem Management

> *Only if we can comprehend and envision the entity we are trying to shape as a dynamic whole can we have any hope of dealing with it creatively.*
>
> J. T. Lyle (1985)

In this chapter, you will learn:

1. **What ecosystem management is**
2. **How and why the concept of ecosystem management developed**
3. **The scientific basis of ecosystem management**
4. **Methods of implementing ecosystem management and what they can accomplish**

12.1. The Concept of Ecosystem Management

12.1.1. What is Ecosystem Management?

One definition of an ***ecosystem*** is *all the organisms in a given area interacting with the physical environment so that a flow of energy leads to trophic structure, biotic* *diversity, and material cycles* (Odum 1971). Put simply, ecosystems are energy- and nutrient-processing systems with physical structures and functions that circulate matter and distribute energy. Although the ecosystem concept dates to the early twentieth century, the idea of *managing* ecosystems is relatively new. Of all modern efforts in conservation, none has proven more elusive in definition or more controversial in implementation than "ecosystem management." As conservationist Michael Bean wrote, "rarely has a concept gone so directly from obscurity to meaninglessness without any intervening period of coherence" (Bean 1997). Less cynically but not more optimistically, Berry et al. (1998) noted that, "No single operational definition of ecosystem management exists, although its basic principles are understood."

Perhaps the location and time closest to the official birthplace and "birthday" of ecosystem management can be traced to the United States in June 1992. At that time, Dale Robertson, Chief of the U S Forest Service, announced that his agency would be moving to an "ecosystem approach" in their management of national forests. Robertson thus made the Forest Service the first environmental agency in the US, and, perhaps, the world, to adopt ecosystem management as its official agency perspective (Butler and Koontz 2005). Within 4 years, 17 other US federal agencies had followed the Forest Service's lead, and had adopted or were considering adoption of programs based on ecosystem management (Christensen et al. 1996; Haeuber 1996; Haeuber and Franklin 1996), producing a wealth of agency-specific definitions of what ecosystem management was (Table 12.1). Such varied expressions of the concept produced more confusion than results, and the need for a clearer definition of ecosystem management was soon apparent. Ideally, that definition would include "all instances and only instances" of what we define and specify as both the essence of the concept and its boundaries so that when we apply the definition, we are able to determine if something is or is not ecosystem management (More 1996). But to frame such a definition, we must consider how the concept developed, and how it is different from past management strategies.

12.1.2. The Historical Roots of Ecosystem Management

From the 1960s, managers of public lands, as well as academics in applied sciences like wildlife management, range management, fisheries, and forestry, spoke and wrote about "ecosystem concepts in management" (Major 1969; Van Dyne 1969; Wagner 1969; 1977). In the United States, the term ***ecosystem management*** had become

TABLE 12.1. Some definitions of ecosystem management in various US federal agencies.

Agency	Definition
Department of Agriculture	The integration of ecological principles and social factors to manage ecosystems to safeguard ecological sustainability, biodiversity, and productivity.
Department of Commerce, National Oceanic and Atmospheric Administration	Activities that seek to restore and maintain the health, integrity, and function of natural ecosystems that are the cornerstone of productive, sustainable economies.
Department of Defense	The identification of target areas, including Department of Defense lands, and the implementation of a "holistic approach" instead of a "species-by-species approach" in order to enhance biodiversity.
Department of Energy	A consensual process based on the best available science that specifically includes human interactions and management and uses natural instead of political boundaries in order to restore and enhance environmental quality.
National Science Foundation	An integrative approach to the maintenance of land and water resources as functional habitat for an array of organisms and the provision of goods and services to society.
Department of the Interior	
Bureau of Land Management	The integration of ecological, economic, and social principles to manage biological and physical systems in a manner safeguarding the long-term ecological sustainability, natural diversity, and productivity of the landscape.
Fish and Wildlife Service	Protection or restoration of the function, structure, and species composition of an ecosystem, recognizing that all components are interrelated.
National Park Service	A philosophical approach that respects all living things and seeks to sustain natural processes and the dignity of all species and to ensure that common interests flourish.
US Geological Society	Ecosystem management to emphasize natural boundaries, such as watersheds, biological communities, and physiographic provinces, and bases management decisions on an integrated scientific understanding of the entire ecosystem.
Environmental Protection Agency	To maintain overall ecological integrity of the environment while ensuring that ecosystem outputs meet human needs on a sustainable level.

Source: US Congressional Research Service (1994). Table design by M. J. Bigelow.

common by the late 1970s (Czech and Krausman 1997). However, when one examines original contexts, authors from this period always used the phrase to describe either the management of populations as commodities within ecosystems or the manipulation of processes, structures, and functions of ecosystems to produce desired levels of animal populations or plant biomass (Major 1969; Wagner 1969, 1977). The modern concept of ecosystem management is different, and what is called "ecosystem management" today represents a genuine transfer of popular, scientific, and professional loyalty from one group of ideas and values to another, in other words, a true paradigm shift. Despite a diversity of approaches, ecosystem management efforts share common goals of maintaining viable populations of native species *in situ*, representing native ecosystem types across their natural range of variation, maintaining normal evolutionary and ecological processes within the system, managing over long time periods, and accommodating human use and occupancy within these constraints (Grumbine 1994).

In all its contexts, ecosystem management has consistently included and stressed three foundational premises: (1) *the ecosystem, not individual organisms, populations, species, or habitats, is considered the appropriate management unit;* (2) *emphasis is placed on use of adaptive management models, which treat the ecosystem as the subject of study and research, and management activities as experimental and uncertain, and* (3) *those with vested interests in the persistence, health and services of the ecosystem (stakeholders) should participate in management decisions*. Therefore, a "classical" definition of ecosystem management might sound something like *a pattern of prescribed, goal-oriented environmental manipulation that (1) treats a specified ecological system as the fundamental unit to be managed; (2) has a desired outcome of assuring the persistence of historical components, structure, function, products, and services of the system within biological and historical ranges and rates of change over long time periods; (3) uses naturally occurring, landscape-scale processes as the primary means of achieving management objectives; and (4) determines management objectives through cooperative and deliberative decision-making by individuals and groups who reside in, administer, or have vested interests in the state of the ecosystem.*

An ecosystem management approach places greater value in the ecosystem itself rather than in the resources it contains. The ecosystem is seen as an object worthy of respect and admiration, valued for its beauty, complexity, history, and cultural significance. Ecosystem management values long-term delivery of ecosystem services, persistence of ecosystem components, and stability (within normal variation) in transfers of matter and energy within the system. Management goals are set by the system's capacity to deliver desired goods and services, not by the demand for those good and services. Because of this shift in value from resource commodities to ecosystems, the ecosystem management paradigm can deal with changing biological and social structures that often have frustrated traditional resource management approaches.

In this context, Grumbine's ten themes of ecosystem management (Grumbine 1994), the Ecological Society of America's eight primary characteristics of ecosystem management (Christensen et al. 1996), and More's (1996) five dimensions of ecosystem management can be see as parallel expressions of similar values (Table 12.2). Ecosystem management is a concept and practice that will take an ever-increasing role in conservation biology. As we grow in appreciation of what populations need to remain viable, include more sectors of human society in conservation effort, and recognize the need for cooperation among management agencies, conservation organizations, and the public, an ecosystem management approach will be essential. But first we must explore why the concept developed at all, and what kinds of problems it attempts to solve.

12.1.3. Development of the Ecosystem Management Paradigm

In the US, federal land agencies have always had jurisdiction *over* ecosystems, but did not historically manage their jurisdictions *as* ecosystems. This distinction can be most clearly understood when parallel elements in the resource management and ecosystem management approaches are directly compared (Table 12.3). Governed by a paradigm of resource management, the entity of value is a particular "resource," either an individual species or an abiotic component of the system such as water, soil, or minerals. The resource is seen as a commodity and its value is "use." Units of management are species or abiotic factors and the sites on which they occur. In this approach, single species are often managed on a site-specific basis, usually through direct intervention. Time scales are short and management decisions occur in individual agencies. The management goal is production of multiple natural resources as commodities for multiple uses, and objectives are determined by demand for commodities the system can supply.

This view of resource management was highly compatible with the traditional bureaucratic organization of most resource management agencies (Figure 12.1a). Organizations like the US Forest Service were arranged as a hierarchical system of supervisor-subordinate control and characterized by departmental organization in which each department had defined jurisdictions and detailed rules governing the roles of agency officials in that department, their operating procedures, and their boundaries of decision making. Policies were set by a "head" accountable to politically appointed or elected officials. Departments were staffed by salaried officials progressing through fixed career lines, which limited communication, understanding, or common interests between

TABLE 12.2. Parallel descriptions of elements of ecosystem management.

The Ecological Society of America's Eight Primary Characteristics of Ecosystem Management (Christensen et al. 1996)		Grumbine's Ten Dominant Themes of Ecosystem Management (Grumbine 1994)		More's Five Dimensions of Ecosystem Management (More 1996)	
Sustainability	Managers aim to create improvements that are not ephemeral.	Heirarchical Context	Managers connect all levels (genes, species, populations, ecosystems, and landscapes).	Recognition of Ecosystem Health	Managers focus on integrity, functions, protection, critical habitats, habitat relationships, and restoration of the ecosystem.
Goals	Managers set goals that specify future processes and outcomes necessary for sustainability.	Ecological Boundaries	Managers are concerned with the ecological boundaries that often cross administrative or political boundaries.	Maintenance and Enhancement of Biodiversity	Managers maintain or restore native/ primeval species and care for old growth and older forest stands.
Sound Ecological Models and Understanding	Managers organize research at all levels of ecological organization.	Interagency Cooperation	Managers interact with the legal mandates and management goals of other agencies to whom they are responsible for a component of the ecosystem (i.e. federal and state officials and private land owners).		
Complexity and Connectedness	Managers recognize that biological diversity and structural complexity strengthen ecosystems against disturbance and supply the genetic resources necessary to adapt to long-term change.	Ecological Integrity	Managers maintain or restore native species, populations, and ecosystems.	Emphasis on Sustainability	Managers holistically consider the long-term effects of their plans.
Wide Temporal and Spatial Scale	Ecosystem processes operate over a wide range of temporal and spatial scales and their behavior at any given location is greatly affected by surrounding systems. Thus, there is no single appropriate scale or time frame for management.			Wide Temporal and Spatial Scale	Managers avoid fragmentation, protect waterways, and focus on landscape-scale trends and conditions.
Humans as Ecosystem Components	Managers value the active role of humans in achieving sustainable management goals.	Humans Embedded in Nature	Managers consider the impact of humans upon the ecosystem and also the impact the ecosystem has on humans.	Legitimacy of Human Dimensions	Managers recognize the need for human communities to utilize some ecosystem resources.
The Dynamic Character of Ecosystems	Managers avoid attempting to halt the evolution of ecosystems.	Monitoring	Managers establish patterns of regular monitoring of ecosystem components and processes.		
Adaptability and Accountability	Managers realize that paradigms and current knowledge are not infallible. Approaches to management are viewed as experiments whose results are carefully examined.	Adaptive Management	Managers are flexible and adapt to uncertainty. Management is viewed as a learning process during which the results of continual experiments are utilized to establish management guidelines.		
		Organizational Change	Management agencies may need to change their structure and the way they operate (e.g., forming an interagency committee, changing professional norms, or altering power relationships).		
		Data Collection	Managers research the ecosystem and collect ecosystem data.		
		Values	Managers keep in mind that human values play a dominant role in ecosystem management goals.		

Source: Compiled from concepts from Christensen et al. (1996), Grumbine (1994) and More (1996). Table design by M. J. Bigelow.

TABLE 12.3. Fundamental differences between resource management and ecosystem management paradigms in entity of value, value application, management units, time scales, jurisdiction, decision making, and management goals.

	Resource Management	Ecosystem Management
Entity of Value	Resource	Ecosystem
Application of Value	Beneficial use	Continuing function
Management Unit	Species or abiotic factor	Landscape elements
Time Scale	Relatively short	Relatively long
Management Jurisdiction	Single government agency	Multiple government agencies and private landowners
Management Decision Making	Single government agency	Multiple government agencies and private stakeholders
Management Goals	Production and use of resource commodities	Productivity and sustainability of ecosystem functions and processes

Source: Table design by M. J. Bigelow.

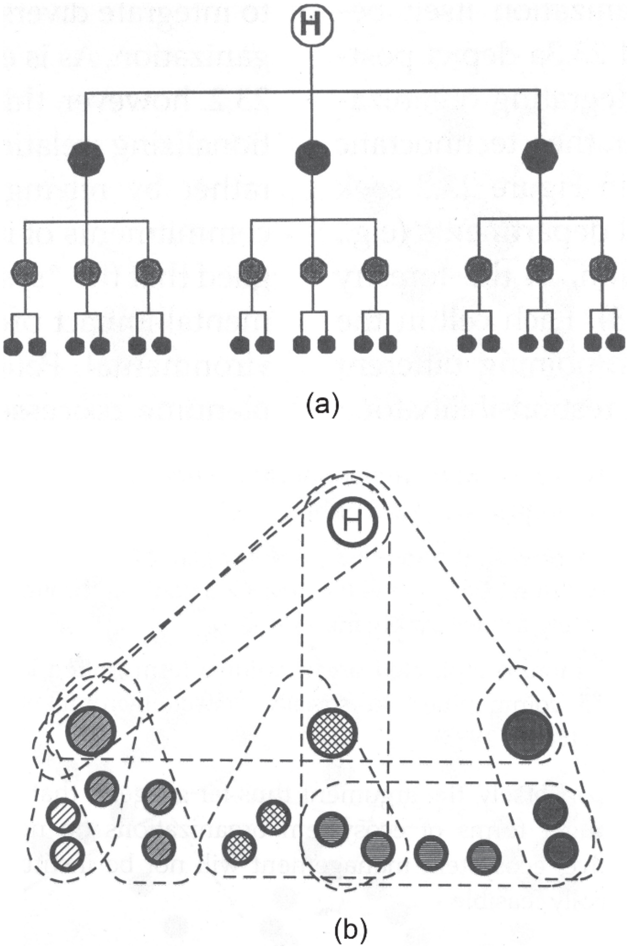


FIGURE 12.1. (a) A schematic organizational representation of a classical bureaucracy in a traditional resource management agency, in which a Head (H) determines policies that are transmitted to lower level employees organized in departments with separate functions and jurisdictions. (b) A schematic organizational representation of a "project organization" model in an agency in which persons and knowledge in different agency areas are shared and fluid according to needs associated with particular project tasks, an organization conducive to ecosystem management approaches. (From *Creating a Forestry for the 21st Century* by Katherine A. Kohm and Jerry F. Franklin, eds. Copyright 1997 by Island Press. Reproduced by permission of Island Press, Washington, DC)

employees following different career paths. Goals were determined at the top and then transmitted to successively lower organizational levels (Meidinger 1997).

Beginning in the 1970s, the resource management paradigm and its attendant bureaucratic structures began to have increasing difficulty in dealing with conservation problems created by new environmental legislation, such as the National Environmental Policy Act and the Endangered Species Act, creating anomalies that helped prepare a climate of acceptance for an alternative approach to management. For example, the Endangered Species Act created a new kind of entity, threatened and endangered species, that could not be managed in traditional ways. As the number of threatened and endangered species increased, species preservation on a case-by-case basis became too expensive to implement and too ineffective in its outcomes to meet the goals of population viability (Franklin 1993; Sparks 1995). Thus, management of endangered species increasingly forced agencies to recognize their deficiencies in expertise needed for management decisions, and compelled them to seek greater cooperation with non-agency scientists and citizens groups. Traditional bureaucratic organizations of agencies also were poorly equipped to deal with the kind of horizontal information sharing and citizen input that new environmental laws stimulated and, in many cases, required, or with the policy adaptability needed for such interaction. Thus government resource management agencies eventually had to change their organizational structures as well as their management models to become functional under these new conditions because their scientists and managers had to begin answering questions put to them by citizens, lawyers, and legislators. To do this, environmental agencies had to begin moving from a bureaucratic organizational model to what could be called a "project organization" model (Figure 12.1b) that was more responsive to local and social concerns. In the project organization model, departments still exist, but individuals and expertise within departments become interchangeable, driven by the demands of individual management "projects" demanding interdisciplinary perspective. Further organizational changes occurred as environmental and conservation dilemmas required expertise and cooperation beyond the agency itself, leading the agency to form more or less permanent relationships with other agencies and non-government entities, the so-called "project organization with external linkages" model (Meidinger 1997). These organizational adjustments better facilitated the kinds of integrative approaches fostered by ecosystem management.

The resource management paradigm also declined because its traditional bureaucratic organization within individual agencies, agency departments, and localized districts could not cope with modern environmental problems, such as air and water pollution, toxic waste disposal, atmospheric deposition, soil erosion, and stream sedimentation, whose sources and impacts exceeded agency jurisdictional powers and boundaries. Further, the resource management paradigm was not able to deal with what could be called the "nationalization" of environmental values. With the emergence of national environmental legislation in countries throughout the world also has come the rise of strong, citizen-based, geographically diverse constituencies that pursued ecosystem preservation for aesthetic and recreational values. Although groups such as The Nature Conservancy, BirdLife International, and The World Wildlife Fund had national organizations, their members also were concerned with local conditions. Agency bureaucracies could no longer justify policies that degraded local environments by simply invoking national policy directives received from the top down or shrug, "We work for Congress and the President," especially when new environmental laws gave citizens ways to pursue their complaints and grievances with an agency, even to the extent of lawsuit.

Thus, changes that fostered the development of ecosystem management were not primarily driven by new scientific information, but by social, legal, and political developments that altered public perception of the environment, as well as fundamental changes that were occurring in how government agencies were organized. As these changes occurred, management actions and results, traditionally viewed as cause and effect relationships, increased in complexity and uncertainty, creating a greater need for rigorous science in the decision-making process. These changes did more than change management goals. They changed the way management decisions were made.

12.2. How Do We Choose What to do? Changing the Decision-Making Process in Ecosystem Management

12.2.1. The Role of Adaptive Management

Ecosystem management is the management of uncertainty, in terms of: (1) unknowable responses and complexities of ever-changing systems; (2) lack of human understanding of the processes and components that determine ecological state; and (3) unreliability of human-collected data and the human biases and limits inherent in its interpretation (Christensen et al. 1996). These uncertainties can not be eliminated, but they can be managed, especially because the effects of the second and third forms of uncertainty can be reduced. Lack of understanding can be reduced through research targeted to ask the most important questions of ecosystem behavior. Biases and human limitations can be constrained with a dedication to high levels of professionalism in the analysis and interpretation of data, careful peer-review of research efforts, and humility about one's own favorite hypotheses and theories (Christensen et al. 1996).

The most important tool in "uncertainty mitigation" is the practice of ***adaptive management***, which has been defined as "the structuring of policy or management actions as a set of testable hypotheses to promote learning from policy implementation, and to allow for greater adaptability when change does inevitably occur within the system" (Lamont 2006:7). That is, adaptive management is a strategy in which the dual goals of system performance and acquisition of reliable knowledge are accomplished simultaneously so that managers intentionally learn about the system through the implementation of their management decisions. An adaptive management approach requires experimental manipulation of the system and a willingness to change research priorities according to management needs. It also requires ongoing interaction with public and private stakeholders to communicate research results in meaningful ways and to learn what stakeholders consider meaningful research.

In adaptive management, management goals and strategies are hypotheses to be tested by experiments. Ideally, management actions should follow investigation based on careful experimental design, include environmental controls (unmanipulated sites or subjects), and be carefully monitored over time. If the experimental design is sound, the results of the management action should be unambiguous, but must still be interpreted stochastically (within a range of outcomes with differing probabilities), rather than as a deterministic outcome generated by simple cause-and-effect relationships.

McClanahan and Obura (1996) exemplified an adaptive management approach by performing an ecosystem-scale "experiment" on African coral reef systems, using Kenyan marine reserves as controls and comparing them to adjacent marine areas open to collecting and commercial fishing. The species richness of coral and fishes was higher in the protected areas, and the differences in species richness between protected and unprotected areas increased with the size of the sampled area (Figure 12.2). Such a study cannot be considered truly experimental because it lacks baseline information (the species richness of the reserve areas was unknown before they became reserves) and additional research is needed to determine the specific causes of decline for particular species. However, such efforts have merit as examples of initial attempts to document differences that ecosystem protection can make, and to begin to identify fishing and collection methods that are most harmful to the diversity of the system. In current management research, these kinds of efforts are being more formally developed as theories of "performance-based

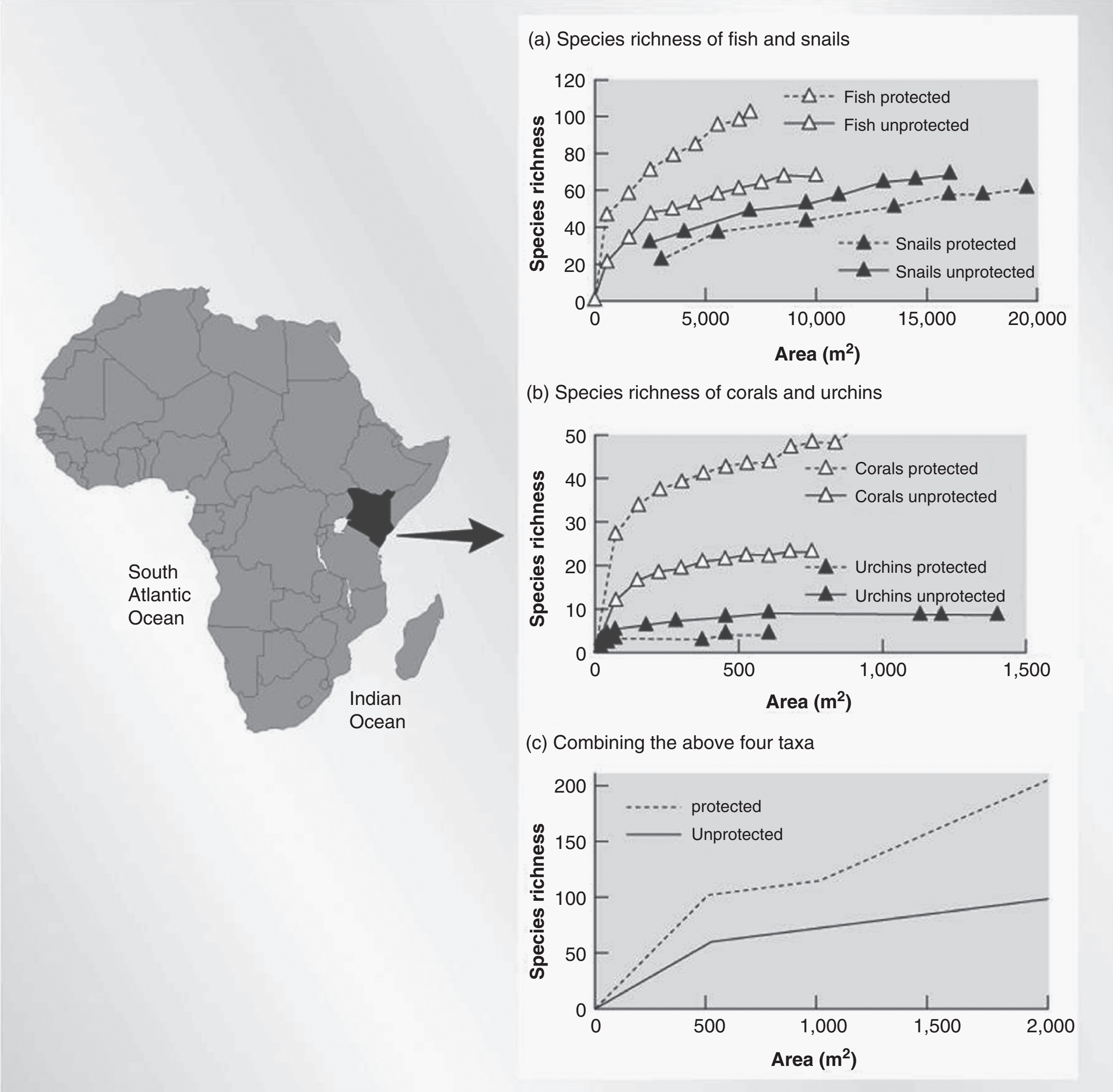


FIGURE 12.2. Species richness in Kenyan marine reserves and adjacent areas open to collecting and commercial fishing. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

management," a concept drawn from the world of business, but with powerful applications in ecosystem management.

12.2.2. Evaluating Ecosystem Management as a Performance-Based System

12.2.2.1. Theoretical Constructs for Performance-Based Evaluation

Like any management system, ecosystem management must measure performance against targets. The question of interest is, what are the targets? Specifically, what variables should be chosen as ***performance indicators***. Such indicators are not simply a way to "score" the success of ecosystem management efforts, but ideally should be part of an overall effort of adaptive management. That is, when indicators reach certain critical states or values this should trigger predetermined management actions. In that sense, performance indicators are reference points that are intended to tell us something about the state of the system. They come in two categories, targets and limits.

Target indicators are appropriate in *production-oriented ecosystem management* when there are significant output functions that the system is managed to produce. Their most common form would be a specified level of stock or biomass of some resource, such as timber or game, that a manager wants to remove or harvest from the system. In contrast, ***limit indicators*** are appropriate in *risk-averse ecosystem management*. Here the prime concern is avoidance of unacceptable risk, such as endangerment of key species. The limit indicator serves as part of an "early warning system" designed to detect or foretell the point where the system begins to come under stress. It would be a measure of a property of a resource, such as recruitment rate, harvest per effort, density, dissolved oxygen level, pH, or other biotic or abiotic metric that, if violated, could be taken as *prima facie* evidence for conservation concern. When the value of the indicator reaches the threshold level, the manager is facing an unacceptable risk of harm to the resource or the system that produces it (Hall and Mainprize 2004).

Target and limit reference points have been compared to a "green light–red light" mentality of management, with "threshold" reference points being the equivalent of a "yellow light" indicator (Figure 12.3). In some cases, the same variable, at different values, can serve as both the target indicator and the limit indicator. Although this kind of system monitoring was originally developed for and is most widely used in fisheries management, it can be applied to any ecosystem management effort as long as the performance measures and reference points meet key criteria. Specifically, the performance indicator must be: (1) *quantifiable*, because a "best estimate" of the indicator is required, along with a measure of uncertainty about the estimate; (2) *simple*, because the indicator must be easy to understand and interpret, not only for managers but for the stakeholders who take part in the decision process; (3) *relevant*, because the indicator must be related to management objectives, such that there is a clear connection between changes in the reference point and changes in the system, not merely a mysterious correlation; (4) *tractable*, so that it can be changed by management action; (5) *faithful*, because the indicator must convey accurate information in every instance, not just in some instances or under ideal conditions; (6) *comparable*, so that the value of the reference point at one time can be compared to its value at other times, even over long periods of monitoring; and (7) *cost-effective*, so that its value can be obtained and actions directed by the value applied without excessive expense (Hall and Mainprize 2004).

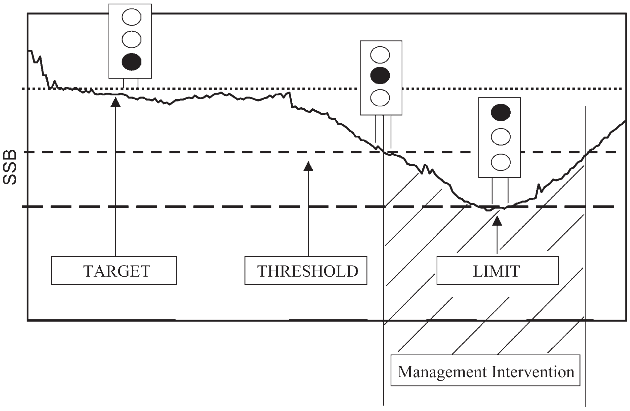


FIGURE 12.3. An illustration of target ("green light"), threshold ("yellow light"), and limit ("red light") reference points that can serve as performance indicators of ecosystem production, function, or risk. In this example, the level of "sustainable system biomass (SSB)" of an unspecified system component serves as the indicator variable. (Hall and Mainprize, Toward ecosystem-based fisheries management, *Fish and Fisheries*, Copyright 2004 by Blackwell Publishing.)

The most important overall considerations in ecosystem management are system biodiversity or ecological functionality. Fisheries managers have taken the lead in developing ways to assess these ecosystem characteristics, and have developed a suite of indicators that can be used to assess system biodiversity or ecological functionality, or that can be used effectively in combination, not only in aquatic ecosystems but also in terrestrial ones (Table 12.4). The question is, can these theoretical and conceptual abstractions be used to identify performance indicators relevant to management actions, and help determine, in advance, what action should be taken if thresholds are reached?

TABLE 12.4. Some measurable ecosystem variables that can be used as performance indicators in ecosystem management.

Properties of Fish and Benthic Communities (Performance Measures)	Metrics (Reference Points)
Biodiversity of Species	
Biomass	Sum of weight across species from survey
Size-structure	Slope of size-spectrum
	Length-frequency distributions of species
	Multi-dimensional ordination
Species identities	Species presence/abundance
	Index of declining or increasing species
	Presence of indicator, charismatic, sensitive species
	Nonindigenous species
Species diversity	Theoretical distribution metrics
	Taxonomic diversity indices
Ecological Functionality	
Resilience	Return time of properties of food webs
	Invasibility
Productivity	P/B ratio
	Carbon per unit area/time/volume
	Partitioning of production between somatic and gonad material
Trophic structure	Connectance
	Path length
Throughput	Internal consumption to yield
	Ulanowiez index
Body well-being	Condition factor
	Incidence of disease, pathogens, parasites, contaminants

Source: Hall and Mainprize, Toward ecosystem-based fisheries management, *Fish and Fisheries*, Copyright 2004 by Blackwell Publishing.

12.2.2.2. The Black-Legged Kittiwake and the Swamp Wallaby

12.2.2.2.1. Kittiwakes, Sand Eels and Performance-Driven Management

The black-legged kittiwake (*Rissa tridactyla*) (Figure 12.4a), a gull-like bird with a widespread global distribution. It is currently listed by the IUCN as "secure," but the regional population of the North Sea has declined more than 50% since 1990, making it a species of increasing conservation concern. Although kittiwakes can be killed by being caught on fish hooks of commercial fishing vessels (because they sometimes try to steal bait from hooks) or entangled in nets or lines, the most significant threat is the reduction of their primary food, the lesser sand eel (*Ammodytes* spp. and *Gymnammodytes* spp.) (Figure 12.4b). Historically abundant, sand eels, which are actually eel-like fish, represent the largest single industrial fishery in the North Sea, and are often a primary food for many sea birds, including kittiwakes. In fact, the breeding success of kittiwake populations, indexed as the number of chicks per nest, is closely correlated with the abundance and availability of sand eels. Certain regions of the North Sea have been declared critical habitat for kittiwakes, and the stakeholders involved in managing the system, namely representatives of the scientific community, fishing industry, and government environmental agencies, have agreed that such regions will be closed to sand eel fishing if the breeding success of kittiwakes falls below 0.5 chicks per nest for three successive seasons. Recently this trigger point was reached in some kittiwake populations, and one area of the North Sea, the Ford of Firth, was closed to sand eel fishing (Hall and Mainprize 2004), and is likely to remain so indefinitely (Frederiksen et al. 2004).

In this example, we see a system in which ecosystem management is both production oriented (harvesting sand eels) and risk averse (avoiding endangerment of kittiwakes). Here, risk aversion trumps production, and concerns for the viability of regional kittiwake populations override concerns to sustain regional sand eel fishing, leading to the management action of fishing season closure on sand eels. Notice that the performance indicator, chicks per nest, meets all seven of the criteria needed to make it an appropriate index for management actions in this system.

12.2.2.2.2. Linking Research Insights and Policy Decisions – The Swamp Wallaby in Australian Forests

If ecosystem management is to have a basis in science and a foundation for professional credibility, it must be able to translate research findings into informed, "on-the-ground" policy at local, site-specific levels of decision making. This requires established and ongoing channels of communication and high levels of trust among researchers and managers. Specifically, managers must know how to place knowledge of ecosystem management processes in the context of existing information. Managers also must work closely with researchers to design and conduct new research to fill knowledge gaps, and determine in advance how to extract high quality information out of management actions by implementing them as experiments. As Australian ecologist Julian Di Stefano astutely observed, "… the existence of ecological data and expertise will not result in improved management outcomes unless positive relationships between ecologists and managers exist" (Di Stefano 2004:62).

In the southeastern Australian province of Victoria, state-administered forests are managed for optimal sustainable timber harvesting, but a common species of herbivore, the swamp wallaby (*Wallabia bicolor*) (Figure 12.5), causes extensive damage to potentially harvestable timber and timber regeneration in recently logged stands through excessive browsing. Swamp wallabies are generalist feeders that spend much of their time in densely vegetated environments, and usually feed close to shelter vegetation (escape cover). Thus, an optimal combination of food and cover define their preferred habitat. Ironically, current harvesting practices used by the Victorian Department of Sustainability and Environment (DSE) often produce near

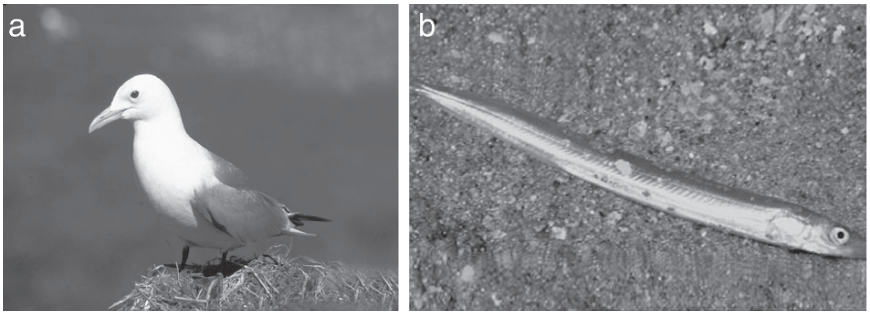


FIGURE 12.4. (a) The black-legged kittiwake (*Rissa tridactyla*) and (b) the sand eel (*Ammnodytes* spp. and *Gymnammodytes* spp.), its most important food. Kittiwake productivity in the North Sea provides ecosystem managers with important performance indicators that generate predetermined management responses that have led to closures of sand eel fishing in sections of the North Sea. (Kittiwake photo courtesy of US Fish and Wildlife Service. Sand eel photo courtesy of Judith Oakley. Copyright Judith Oakley (www.oakleynaturalimages.com))

FIGURE 12.5. The swamp wallaby (*Wallabia bicolor*), a species which provides ecosystem managers with performance indicators based on its level of browsing damage and effect on regeneration of tree species in harvested areas in Australian forests. (Photo courtesy of Rainer Richter. Copyright Rainer Richter 2007.)

optimal habitats for swamp wallabies on logged sites in which the wallabies' favorite food (seedlings and other regenerating plants) grow close to dense cover vegetation. Thus, changing harvesting procedures and silviculture manipulations might reduce the browsing problem. Di Stefano, an ecologist with the DSE, planned an adaptive management study focused on answering these questions: (1) How widespread was the problem of excessive browsing of regenerating timber by swamp wallabies? (2) Were there ecological and habitat factors that could be used to predict browsing damage before it occurred? (3) Were current browsing reduction strategies meeting management objectives? (4) If not, what new browsing reduction strategies might be appropriate?

As with kittiwakes and sand eels, we see in these Victorian forests a management system that is simultaneously concerned with two criteria. It is production oriented (for sustainable timber harvest), and therefore concerned with performance indicators that measure production levels, such as the rate of forest regeneration in logged stands. At the same time, it is risk averse (desirous to prevent unacceptable browsing levels on timber by wallabies), and therefore interested in determining threshold values of browsing that would indicate critical stress to the system's ability to produce new timber. The performance indicator is the level of browsing that reduces regeneration of trees below the level at which the stand can regenerate, a classic "threshold value." Here production and risk are linked in the same indicator, regeneration rate. Thus, Di Stefano noted, "Objective determination of an acceptable browsing level provides a scientifically defensible trigger for management action, and requires linking early damage levels with an accepted regeneration standard. If browsing results in a failure to meet the regeneration standard browsing may be considered unacceptable" (Di Stefano 2004:63).

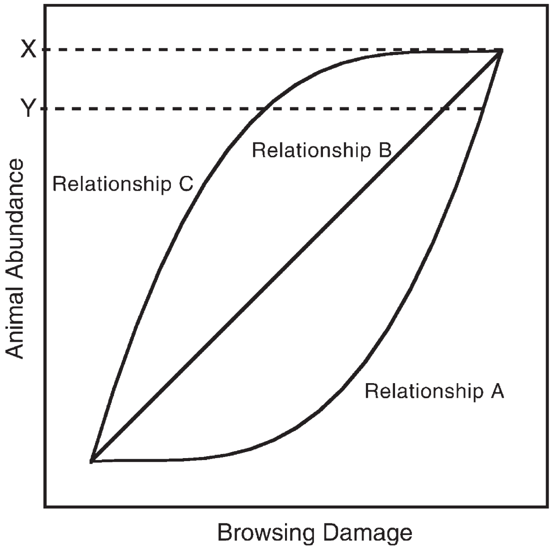


FIGURE 12.6. Three theoretical threshold relationships between browsing damage and animal abundance that could hypothetically apply to the effect of browsing by swamp wallabies on forest regeneration in Australia. In (A), animal abundance must be greatly reduced to observe significant reduction in browsing damage. In (B), animal abundance and browsing damage vary directly and proportionally. In (C), a small reduction in animal abundance leads to a disproportionately large reduction in browsing damage. (Di Stefano, The importance of ecological research for ecosystem management: the case of browsing by swamp wallabies (Wallabia bicolor) in commercially harvested native forests, *Ecological Management and Restoration*, Copyright 2004 by Blackwell Publishing.)

The relationship between the abundance of wallabies and browsing damage could take several forms, as shown in Figure 12.6. If the relationship follows curve A, reducing the level of wallabies from abundance X to abundance Y would have little effect on the amount of damage done to the stand by browsing. If curve B, the relationship is direct and proportional, such that every unit of reduction in wallabies results in a proportional unit reduction in browsing damage. If curve C, a small reduction in wallabies would lead to a disproportionately large reduction in browsing damage. The goal of the experiment is to apply different levels of wallaby removal in different areas, measure the associated regeneration response, and see which pattern the data fit.

At the time of its publication, Di Stefano's study had not yet completed the research needed to answer the questions posed. But Di Stefano points out some of the obstacles to achieving the connectedness between research and management that he advocates, noting "… the responsibility lies with members of both professions. In many circumstances, ecologists are focused on pure, process-based research and pay little attention to how their work could be usefully used in a management context … managers set the agenda and define the problems … and thus are in the best position to facilitate collaboration between the disciplines … [but] managers often fail to consult ecologists when this would have clear benefits for management outcomes" (Di Stefano 2004:65).

Because government agencies employ both managers and ecologists, they are in an excellent position to facilitate the kind of change Di Stefano describes. The question is, will they? That query is not unique to Australia, but must be addressed in the global conservation effort if ecosystem management is to become a workable process that advances conservation strategy and long-term ecosystem sustainability.

POINTS OF ENGAGEMENT – QUESTION 1

Consider two dimensions of "Di Stefano's Dilemma." First, design an experiment that would determine the relationship between stand regeneration and wallaby browsing. Second, design a model of organizational structure in the Victorian DSE that would make it easier for managers and researchers to work together in designing the experiment and for transferring and applying the data gained from it to management action.

12.2.3. Stakeholder Participation in Ecosystem Management

It is one thing to talk about ecosystem management, or even take the trouble to carefully define it. It is quite another to do it. As noted earlier, ecosystem management not only requires a different set of management actions to be successful, it requires a different kind of *managing process*. Precisely because ecosystem management involves the management of ecological processes over large landscape scales that routinely exceed the jurisdictions of individual agencies, management decisions must incorporate decision-making strategies that involve all agencies with jurisdiction over lands or processes in the ecosystem, as well as private landowners within or adjacent to the system, and non-residents who use the system on a seasonal basis or who have specific and vested interests in the state of the system. Ecosystem management also must integrate ecological and social information at a variety of levels. Further, most ecosystem management efforts must coordinate management activities on separately owned and multiply governed lands, often with conflicting mandates (both apparent and real), and managers must support ongoing dialogue with the community to evaluate different management and policy options, build community understanding of ecological issues, and then choose the best course of action informed by stakeholder deliberation.

In this kind of management approach it is essential to identify and include non-agency stakeholders in the decision-making process. But who are these stakeholders? We can define ***stakeholders*** as *individuals or groups possessing vested interests in the persistence, health, products, state, or services of a system to whom managers have legitimate and defined functional, ethical or legal obligations*. But it is not enough to identify stakeholders. Managers also must form partnerships with them to ensure their involvement in decision making and to create support for management actions. We should understand ***partnerships*** specifically as *dynamic relationships among actors, based on mutually agreed upon objectives, pursued through an understanding of division of labor based on the respective comparative advantage of each member* (Brinkerhoff 2002), not casual associations of people who happen to attend the same meetings.

Stakeholder involvement and partnership is an attractive vision to hold, but a difficult goal to attain. To be successful, an ecosystem management effort must achieve a collaboration that leads to a common vision of desired future conditions, not just a roundtable discussion. This vision must not only incorporate ecological science, but also successfully integrate social, economic, and community-based perspectives. Nevertheless, science remains the foundation of the ecosystem management effort because it gives all participants shared understanding of how the ecosystem actually functions. To understand that foundation better, we now explore that scientific basis.

12.3. The Scientific Basis of Ecosystem Management

12.3.1. The Problem of Location – Where is the Ecosystem?

Ecosystem management is challenging because it attempts to manage a constantly changing entity. As Berry et al. (1998) noted, "There exists a large gap between the operational needs of those responsible for ecosystems management and the knowledge required to meet those needs." To understand how ecosystems change and how such change might be managed, an ecosystem manager must determine: (1) the physical boundaries of the system to be studied, the fundamental landscape units within the system, and the spatial and temporal scales at which they should be studied; (2) how to construct meaningful ecological models of the system; (3) how to collect and monitor relevant data at scales appropriate to the system and its model(s); (4) how to identify, measure, and manage the most important processes, both natural and anthropogenic, affecting the transfer of matter and energy in the system; (5) how ecological processes interact with landscape processes and scales; and (6) how to design and conduct small-scale experimental manipulations within the system to test predictions of the model(s) and determine likely responses to natural disturbances and management practices.

Just as a general definition of ***ecosystem*** can be elusive, the particular limits of an individual ecosystem to be managed can be hard to define, even when there are no jurisdictional constraints and when the best available scientific information is employed. Ecosystems have notoriously "leaky" boundaries. They are open systems, not closed to gains or losses in terms of organisms, matter, and energy. Different agencies and individuals approach the problem of ecosystem definition in a variety of ways, depending on ecosystem characteristics and management objectives.

Traditional political delineations are the easiest way to delimit boundaries of an ecosystem, and may have the attraction of placing the management area under a single administrative jurisdiction, or at least under a group of related jurisdictions. Unfortunately, this method of delineating the ecosystem is almost never meaningful because ecological processes rarely match the borders of management jurisdictions. Examples of the shortcomings of politically-based ecosystem designations are as numerous as they are depressing. One of the most tragic is the case of the Everglades ecosystem of south Florida (USA). The combined holdings of the Everglades National Park, the Big Cypress National Preserve, Biscayne National park, three water conservation areas (WCAs), and numerous smaller state and private reserves protect about 67% of the land area of the original ecosystem. But, although the majority of the Everglades land area was protected, its water flows were not. The construction of 2,200 km of canals and levees, over 40 pumps and spillways, and the impoundment of neighboring Lake Okeechobee to the north permanently altered the amount and timing of water through the ecosystem, causing long-term, severe degradation (Lockwood and Fenn 2000). A long-embattled, but finally approved restoration plan will require a multi-billion dollar effort spent over a period of more than 30 years.

In conservation management, many have begun to define the ecosystem as collections of watersheds within a defined area or that empty into a common source (D'Erchia 1997; Norton and Davis 1997; Rama Mohan Rao et al. 1999; Richardson and Gatti 1999). For example, managers in India divided the country into 20 land resource regions (LRRs) and 186 land resource areas (LRAs) based on an integrative assessment of differences in soil, rainfall, forest cover, land use practices, water resources, and elevations. This system was refined to 17 soil conservation regions classified according to climate, rainfall, mean annual temperature, elevation, watershed boundaries and land use (Table 12.5; Rama Mohan Rao et al. 1999). In Wisconsin (USA), managers used watersheds as the fundamental unit in an ecosystem management approach to restore drained agricultural wetlands (Richardson and Gatti 1999). Using a geographic information system (GIS), the managers in Wisconsin combined satellite imagery with information on wetlands from state and federal wetland inventories to produce an integrated, digitized database that was used to identify wetlands and account for changes in wetland status over

TABLE 12.5. Major characteristics of soil conservation regions in India that serve as a basis for defining watershed-based management, one practical approach to defining ecosystems for ecosystem management. Watershed boundaries and land use not included in this table.

Region	Climate	Rainfall (Cm)	Mean Temp (°c)	Growing Period (Degree Days)
Glacier	Cold arid	0–100	<20	0–90
Karewas	Cold semidarid (dry) to humid and perhumid	60–250	20.0–22.5	90–300
Shiwalik	Semiarid to humid and perhumid	20–150	20.0–27.5	120–300
Indogangetic Plain	Subhumid dry to subhumid moist	100–150	22.5–27.5	180–210
Arid	Typic/arid to hyperarid	5–50	25.0–27.5	0–90
West Alluvial Plain	Semiarid dry to semiarid moist	50–150	25.0+	90–150
Beehar	Semiarid dry to moist	40–150	22.5–27.5	120–180
Southern Malwa	Semiarid moist to subhumid dry	75–150	22.5–27.5	120–150
Plateau	Semiarid dry to semiarid moist	75–150	20.0–27.5	90–150
Chalka	Arid (typic) to semiarid moist	50–250	20.0–27.5	60–150
Western Ghat	Subhumid to perhumid	100–250	25.0–27.5	240–270
Central Eastern Upland	Subhumid dry to subhumid moist	75–150	22.5–27.5	150–180
Eastern Ghat	Semiarid dry to subhumid dry	100–150	25.0–27.5	120–210
Diara	Subhumid dry to subhumid moist	100–150	25.5–27.5	150–210
Sundurban and Eastern Valley	Subhumid dry to perhumid	100–150	20.0–27.5	210–300
North Eastern Hill	Humid to perhumid	150–250	20.0–22.5	270–300
Island	Humid to perhumid	160–300	20.0–28.0	240–300

Source: Based on data from Rama Mohan Rao et al. (1999). Table design by M. J. Bigelow.

the previous 12 years. Wetlands were then ranked based on rates of soil loss, and sediment delivery of all wetlands within a watershed was summed. In this case, restoration of upper-elevation wetlands proved to have the greatest effect on lowering water velocities to all downstream sites, greatly reducing erosion and sediment delivery to downstream areas (Richardson and Gatti 1999).

12.3.2. The Problem of Information – What Data Should Be Collected and Interpreted for Ecosystem Management?

12.3.2.1. General Considerations

Ecosystem managers face difficult choices about which information to collect and how to interpret it. There is an abundance of general-purpose data on ecosystem management, but information that meaningfully relates such data to actual management decisions and provides reliable system performance indicators is scarce. Recognizing the value of the latter kind of information, some have gone so far as to demand that ecosystems should not be managed without establishing "quantitative and measurable standards of ecosystem structure and functions" (Wagner and Kay 1993:268). This expectation is not realistic. Fluctuations in ecosystem structure, processes, and component populations are great and often unpredictable (Boyce 1998). Ecosystems are large units encompassing multiple jurisdictions and categories of land ownership. The types of data that are gathered, stored, and desired by different agencies and stakeholder groups are diverse and usually uncoordinated. For example, the US EPA commissioned an independent review group of scientists in 1995 to assess the current status of ecosystem management research in the US Pacific Northwest. After a comprehensive review of published and unpublished literature, interviews with and extensive surveys of scientists, managers, interest groups, and national policy makers involved in the area, and in-depth conversations with focus groups of all of the above, the scientists came to a discouraging conclusion: *no main source of ecosystem management research information exists in the Pacific Northwest region* (Berry et al. 1998). Shocking as this finding is, we would be naïve to suppose that there are many places in other parts of the world that are in better shape. Thus, managers often are caught between those demanding an impossible standard of ecosystem knowledge and the reality of inter-agency un-coordination that does not even know where the information has been filed. But even such formidable challenges are not insurmountable. There are ways to overcome these problems.

Managers may not always be able to define "quantitative and measurable standards," but neither are they doomed to futility because of poor inter-agency coordination. Managers can take the initiative to make intelligent and informed decisions by consistently collecting, monitoring and reporting appropriate ecosystem data at appropriate scales. From such information, they can determine the range of fluctuations of ecosystem processes and components in different systems, and whether existing data in their system are within those ranges. Several important methodologies and types of data – both old and new – exist to help achieve ecosystem management goals.

Biological data have been used to evaluate the health of some ecosystems. The Ohio (USA) Environmental Protection Agency (EPA) developed a monitoring and assessment program of streams that uses biological and chemical data to define and assess water quality. Repeated biological surveys provide baseline criteria to judge water quality and overall ecosystem health. Indices for "normal" or "healthy" ecosystems were derived from sampling at 300 minimally impacted sites. Fish and macroinvertebrate data were used to establish attainable, baseline expectations for different habitats and ecoregions across the state. Using chemical data alone, nine percent of sites failed to meet water quality standards. With the addition of biological data, 44% failed (Norton and Davis 1997). Based on these results, the Ohio EPA has affirmed that biological components are key indicators of ecosystem health and continued to use them in defining water quality standards. Although such indicators are not yet fully linked to the performance-based management strategies we have reviewed earlier, they are useful in making assessments of the system's overall condition and monitoring it over time.

One objective way to determine ecosystem health is by identifying the presence of ecological stress and the system's response. Because ecosystems are successional in nature and often show signs of stress only over relatively long periods, long-term data are needed to evaluate ecosystem condition. There are five kinds of long-term data available for ecosystems: (1) regularly collected data; (2) remotely-sensed data adaptable to GIS (3) archived data from previous studies; (4) data from long-term natural repositories; and (5) data from preserved areas within the ecosystem not subjected to disturbance.

12.3.2.2. Regularly Collected Data

Regularly collected data, sometimes incorrectly called "continuously collected data," are obtained from surveys or samples that measure the same variables, at the same locations, at regular intervals. For example, in specific regions and ecosystems, vegetation data are often collected at annual or otherwise regular intervals along permanently established transects. The historic "Parker transects" of Yellowstone National Park (USA) have provided estimates of range condition in the park since 1954, although some measurements were begun as early as the 1930s (Coughenour et al. 1994). Measurements taken inside

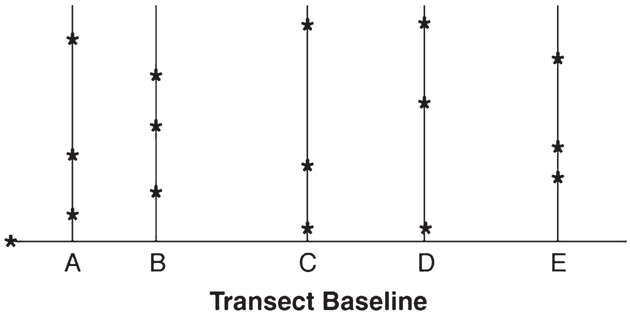


FIGURE 12.7. A schematic diagram of one way to establish a baseline with randomly selected sampling transects and sample plots. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

and outside of long-established exclosures (wire pens that exclude ungulates) have helped to determine the long-term effects of grazing and browsing of ungulates on plant communities. Similarly, McInnes et al. (1992) used exclosures established on Isle Royale National Park in Michigan (USA) between 1948 and 1950 as controls to evaluate the effects of moose browsing on forests.

Where long-established transects or other sampling units do not exist in an ecosystem, managers are well-advised to establish them using standard survey/census methods within a well-conceived design and to begin regular sampling and monitoring. Random or systematic sampling points can be chosen by using a landscape grid to ensure that: (1) samples are chosen randomly or systematically; (2) samples are representative of the entire area; and (3) adequate numbers of sites are sampled (Figure 12.7).

Although grid sampling can provide large amounts of data, it has many problems. Any particular grid assumes that the sampled environment is relatively homogeneous at the sampling scale. Where the environment is obviously heterogeneous, multiple grids are necessary, one for each kind or category of landscape or ecosystem encountered. As grids or sampled points within grids multiply, sampling becomes increasingly labor intensive and costly. In remote ecosystems, some randomly selected sampling points may be difficult to reach. There will be tension between the number of variables sampled at each grid point and the number of grid points that can be sampled. Sampling more variables provides more site-specific information, but the increase in time investment per point reduces the sample size and reliability of observed differences. Because of this tension, some ecologists advocate giving more attention to which variables to sample rather than maximizing the number of grid points (Loehle 1991).

The historical practice of collecting information from such sampling points directly through field observation invariably led to under-informed management because limits of costs and manpower were reached quickly in such time- and labor-intensive methods, especially in historically under-funded environmental agencies. Today long-term, regularly collected data acquisition and analysis are facilitated by remote sensing techniques, continuously operating recording equipment ("data loggers") and GIS.

12.3.2.3. Ecosystem Management and Geographic Information Systems – How Technology Enables Management Purpose and Strategy

In a real sense, ecosystem management was not possible prior to the development of remote sensing, whereby satellites orbiting the Earth provide information on a multitude of environmental variables. The primary sources of satellite imagery used for analysis of biological data at geographic scales are Landsat TM satellites, designed for high-resolution photography and arranged in orbits so as to systematically photograph all parts of the Earth's surface at regular intervals. When visually enhanced and their spectral images digitized, such photographs yield vast amounts of information, especially when integrated through technologies of GIS.

A GIS is a computer-assisted system designed for the acquisition, storage, manipulation, analysis, and display of geographic data. It consists of multiple pieces of integrated software that, together, can solve complex problems in spatial analysis (Figure 12.8). Additionally, a GIS can process complex images, such as aerial or satellite photographs, to yield more information than could be acquired by human visual perception alone. Among the most common and important uses of GIS are: (1) creating data management systems for geographic information that allow users to enter "attribute data" (e.g., elevation, soil type, vegetative cover, land use, and other variables) into files that can then be manipulated to display such data in new ways that are geographically or spatially sensitive; (2) determining and displaying the union and intersection of different geographic and biological variables through virtual, computer generated overlay maps; (3) organizing and displaying the distribution of geographic, climatic, or biologic patterns at large scales (e.g., regional, continental, or world, Figure 12.9); (4) converting raw remote sensing data to digital information that can be redisplayed as an interpretive map using prescribed classification procedures; (5) performing statistical analyses of geographic information; and (6) providing "decision support systems" that use pre-programmed decision rules and criteria to assist managers in making decisions about land use or resource allocation, visually represented by "multi-criteria suitability maps" that can indicate the best management practices on particular land areas, such as the kind used by The Nature Conservancy for aquatic ecosystem conservation as described in Chapter 11.

To display such unions and intersections, GIS programs can construct maps of the same area for different variables

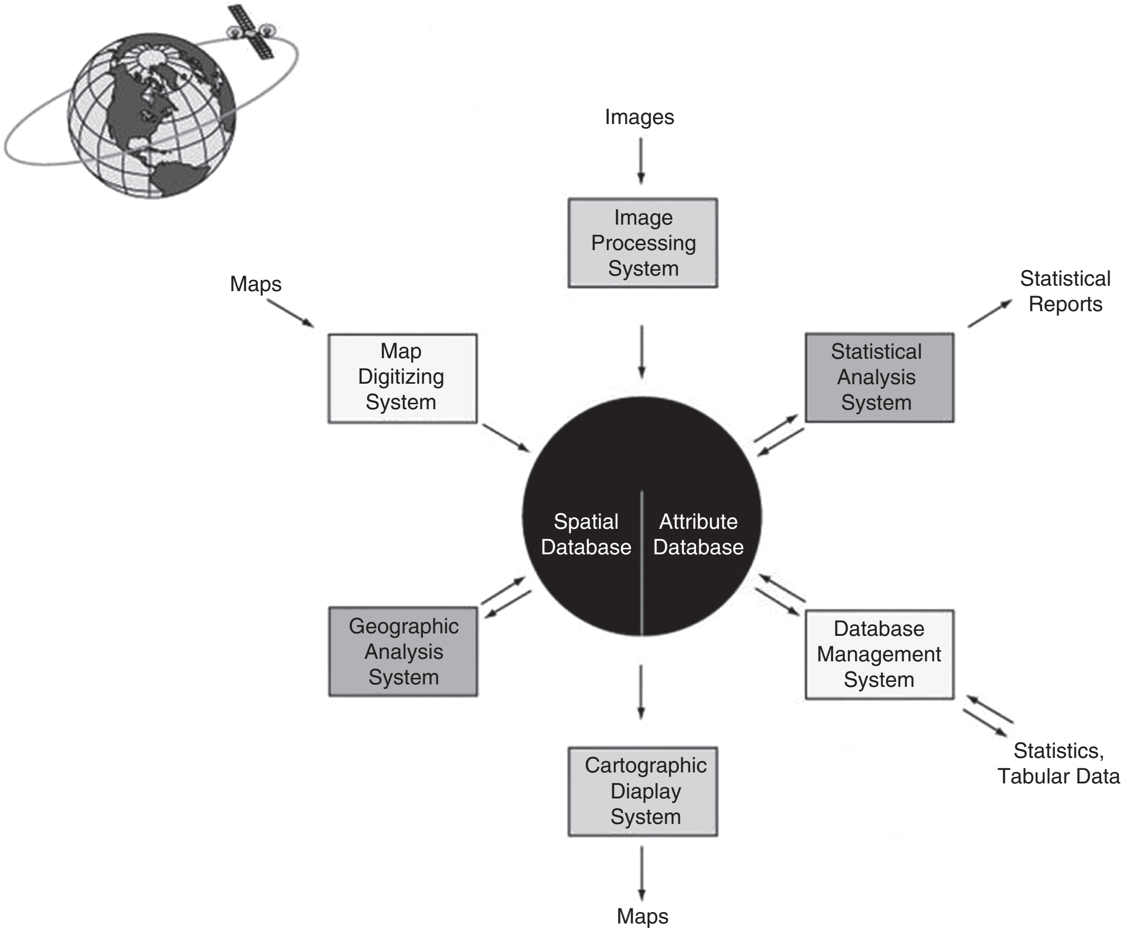


FIGURE 12.8. The conceptual organization of a geographic information system (GIS) in terms of components, relations and outputs. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

(for example, soils, vegetation, and elevation), and then create a single virtual overlay map that shows the union and intersection of different variables with one another. Using such a map, potential habitats for species whose environmental tolerances require a union of multiple variable states (for example, vegetation, elevation, and moisture) can then be identified, as they were by Rondinini et al. (2005) to develop range maps for African vertebrates, as discussed in Chapter 10.

Satellite images or aerial photographs can be used to identify vegetation or land-use types based on the spectra they emit. From this information, an appropriately constructed GIS program can determine the proportion and quantity of areas associated with different land-use practices or habitat types, a first step in an ecosystem inventory. For example, Shinneman et al. (2000) used a GIS to determine the relative level of ecosystem protection in the southern Rocky Mountains of the United States. They first converted existing vegetation maps of the region into GIS formats and then used GIS to reclassify the vegetation into 13 types of regional ecosystems. They created a separate map showing the boundaries of "land stewardship categories" that represented different levels of protection for each land area and closely followed existing Gap Analysis Program (GAP, Chapter 10) categories in that region. In addition to the land stewardship categories, existing GIS maps on GAP also integrated occurrence of rare and endangered species. Recall that GAP is a national effort to identify "gaps" in biodiversity protection by integrating maps of natural vegetation with distributions of species (D'Erchia 1997). By creating an overlay map that showed the union and intersection of the land stewardship categories and ecosystem types, integrated with rare and endangered species associated with such ecosystems, Shinneman et al. (2000) were able to use GIS to determine the area of each ecosystem associated with each stewardship category.

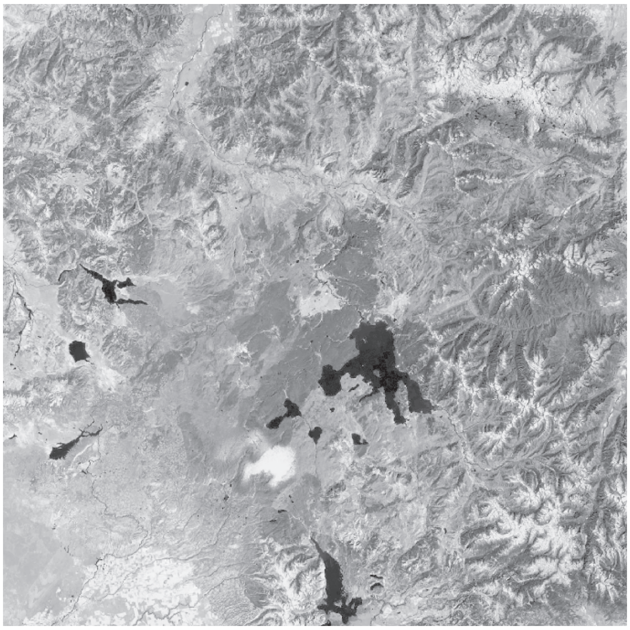


FIGURE 12.9. A satellite photograph of Yellowstone National Park, Wyoming (USA) taken on July 22, 1988, illustrating the type of remotely sensed data that can be used by a geographic information system (GIS) to analyze ecosystem, landscape and habitat characteristics on local, regional, or global scales. (Photo courtesy of NASA Visible Earth (http://visibleearth.nasa.gov))

GIS also can use data from long-term ecological research (LTER) program sites to detect historical changes in ecosystems. D'Erchia (1997) used GIS to compare land-cover changes along the Upper Mississippi River (US) at LTER sites associated with impoundments constructed on the river from 1891 to 1989. This effort permitted an analysis of the effects of levee placement on habitat, floodwater levels, and sedimentation rates in this ecosystem over an extended period of time.

POINTS OF ENGAGEMENT – QUESTION 2

Ecosystem Management developed partly in response to the increasing complexity of environmental problems and to shifting public attitudes toward the value of ecosystems. Was its development and acceptance also facilitated by the development of remote sensing and GIS technologies that were occurring at about the same time? How, in your view, did technological opportunity, management need, and public sentiment interact to facilitate development of the ecosystem management concept?

12.3.2.4. Archived Data and Historical "Experiments"

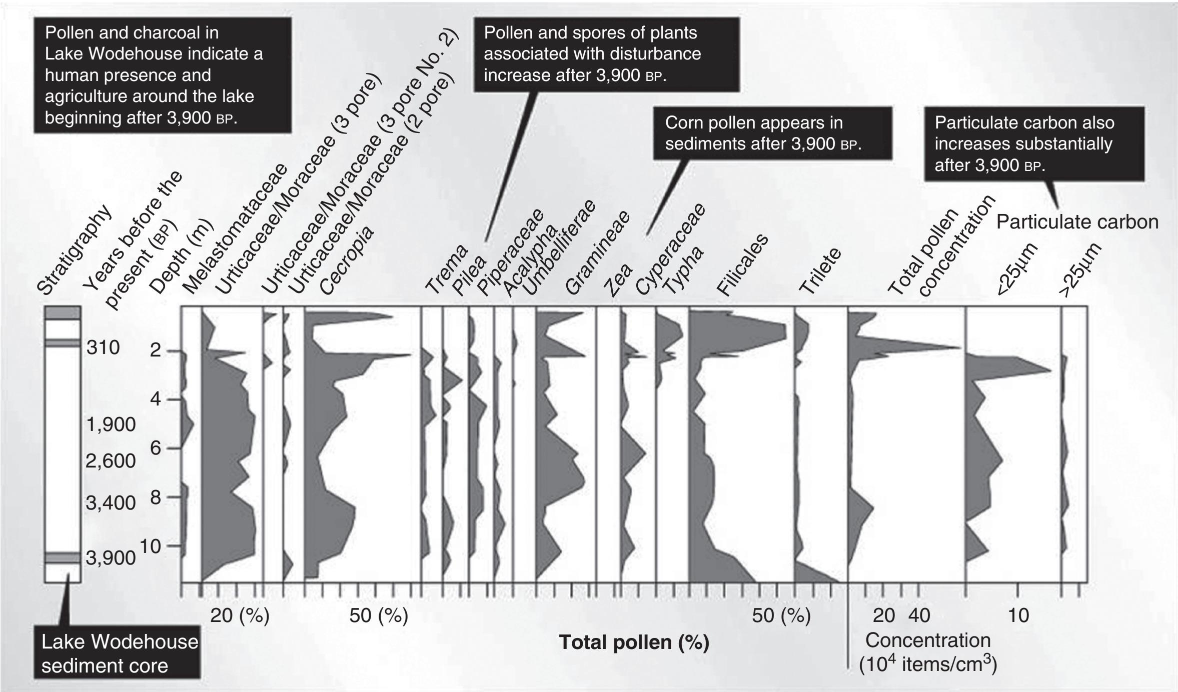
Another important long-term comparison and evaluation is the examination of archived data available from past studies of ecosystems. In the US and many other countries, areas where all or part of the ecosystem have a long history of public ownership and agency jurisdiction often have a long history of ecological investigations. Many such investigations take the form of unpublished reports, unprocessed data in agency files, personal journals, historical photos of the ecosystem at various sites, herbarium records that document the location and occurrence of plant species, soil surveys, and geologic maps, past aerial photos, as well as peer-reviewed published literature. Although such archived data may vary in quality and almost always require extra effort in analysis and interpretation, such information can be extremely valuable. This kind of search and interpretation of past data and records (often referred to within agencies as ***data mining*** or ***mining of legacy data***) is always essential for ecosystem inventory and establishing ecosystem baselines for comparison to current conditions and states. For example, Chadde and Kay (1991) compared historical and contemporary photos from the same sites to document decline of tall willow communities in Yellowstone National Park from the late 1800s to the present (Figure 12.10).

FIGURE 12.10. Yancey's Hole on the northern range of Yellowstone National Park, Wyoming, USA. In 1915 (left photo), tall willow (*Salix* spp.) communities are prominent at the site. At the same spot in 1987 (right photo), willows are absent. (1915 photograph (left) courtesy of Charles C. Thomas, Publisher, Springfield, Illinois. 1987 photograph (right) courtesy of Charles E. Kay.)

12.3.2.5. Data from Long-Term Natural Repositories

Not all archives are found in file cabinets, field journals, or old photograph albums. An ecosystem keeps its own records that can provide documentation of past events, if one knows where to look. Lake and bog sediments, for example, provide long-term records of biological change in ecosystems compiled over periods of hundreds or thousands of years. Such sediments are repositories of pollen grains that are dispersed annually by plants. Pollen grains are resistant to decay and distinctive by species, and their proportional abundance in sediments, appropriately corrected for differences in pollen production by different species, gives an index of the proportional abundance of plant species around the lake or bog. Properly extracted, a core of sediment provides a "profile" of the abundance of different species of pollen deposited in the lake over time. As the abundance of pollen of different species changes, one can make inferences about changes in the ecosystem, and estimate the time period associated with such changes if one can accurately estimate the rate of sediment deposition. Notice, for example, how the relative abundance of different pollen types changes in the sediments of a Panama lake (Figure 12.11). Sediments also keep careful records of material that precipitates from the surrounding water and air. Two such precipitates are ash and charcoal, substances usually produced by fires. From the abundance and depth of these materials in lake and bog sediments, one can infer the relative frequency of fire in the surrounding ecosystem over an extended period of time.

A special category of "long-term natural repositories" is sometimes found in undisturbed areas, which can provide baseline information used to compare responses in systems stressed by varying kinds of disturbance. Nature preserves or other specially protected areas within an ecosystem serve as controls or "before impact" sites when evaluating ecosystem status and change; they are what some ecologists call "time-control substitutes" (Loehle 1991). Ecosystem structure and function in these sites can be compared to otherwise analogous disturbed sites within the ecosystem to determine how the system has changed over time in response to the disturbances that affect it. Such comparisons can be helpful, but require careful interpretation and many qualifiers. Regional sources of disturbance, such as air pollution, water pollution, or invasive species, may affect all sites regardless of their "protected" status. Multiple types and levels of disturbances may affect unprotected sites, so differences between them and protected areas are unlikely to be traceable to a single cause. Finally, protected, undisturbed sites are often smaller than surrounding unprotected areas. As discussed in Chapter 10, ecological structure and function may be adversely affected by fragmentation and edge influences, which are more pronounced in smaller reserves.



Pollen and charcoal in Lake Wodehouse indicate a human presence and agriculture around the lake beginning after 3,900 BP.

Pollen and spores of plants associated with disturbance increase after 3,900 BP.

Corn pollen appears in sediments after 3,900 BP.

Particulate carbon also increases substantially after 3,900 BP.

Lake Wodehouse sediment core

FIGURE 12.11. Pollen and particulate carbon in the sediments of Lake Wodehouse, Panama, dating from the present to 3,900 years before the present (BP). (Data from Bush and Colinvaux 1994. Figure courtesy of Ecological Society of America.)

12.4. Implementing Management Decisions – What are the Tools of Ecosystem Management?

12.4.1. Ecosystem Modeling

Ecological modeling has been described as "indispensable and always wrong" (Lee 1993). A ***conceptual model*** is a visual or narrative summary that describes or identifies important components of a system and the possible interactions among them. Conceptual models can illustrate the interconnectedness of ecological processes, both as they occur in nature and as they respond to anthropogenic influences. Conceptual models help to identify how major drivers and stressors will affect ecosystem components (Barber 1994) and provide a framework for communication among scientists and managers from diverse disciplines (i.e., they serve as cross-disciplinary heuristic devices) (Allen and Hoekstra 1992). The latter function is especially important in avoiding the disconnect common between managers and researchers illustrated in our earlier example of the management of the swamp wallaby in Australian forests.

In contrast to conceptual models, simple ***compartmental models*** serve to organize information and express connections and relationships among ecosystem components more explicitly. Still more complex ***simulation models*** involve the mathematical estimation of many state and transition variables through time and across landscapes (Christensen et al. 1996). Models specifically designed for use in ecosystem management typically serve at least one of the following functions.

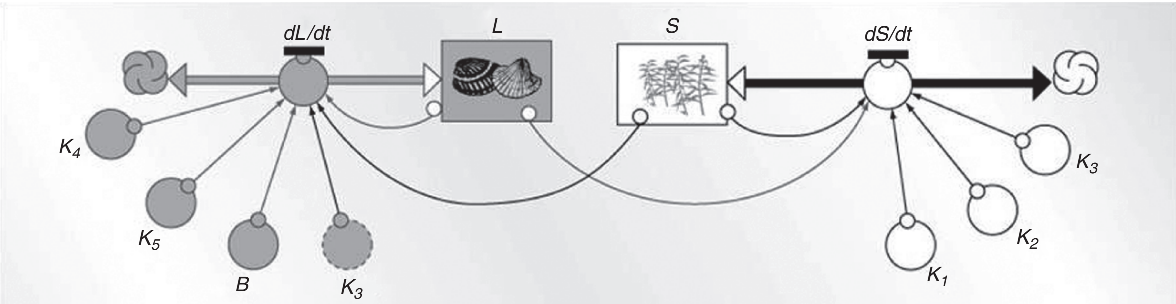
1. *Prediction models* estimate the outcome of individual actions or decisions using mathematical or conceptual relationships.
2. *Research coordination models* include factors that each research effort studies and identify the relations between the research efforts.
3. *Policy evaluation models* explore different management scenarios through simulation by evaluating an array of different management actions.
4. *Institutional memory models* inform future scientists and managers of the workings of the system as their predecessors understood it.
5. *Management training models* train decision-makers in anticipating possible responses of the systems they manage to the actions they may take.
6. *Optimization models* determine the "best" action to achieve a particular objective.
7. *Hypothesis testing models* provide statements of a scientific hypothesis and means of comparison between the hypothesis and other models and data (Hillborn 1995).

Model forms and parameters are chosen by determining issues the model should address, appropriate indicators of system performance, management actions that may be considered, spatial and temporal measurement scales, desired resolution, model components, and appropriate flow of information among components (Hillborn 1995).

Although models defer in detail and purpose, ecosystem managers must define the values of five types of entities to build a working model. ***Stocks*** refer to amounts of levels of a variable of interest that the model counts or monitors. ***Sources*** and ***sinks*** are entities from which the stock originates (sources) or into which the stock is absorbed (sinks). ***Flows***, generally expressed as equations, determine rates of movement of stocks to and from sources and sinks or, in some cases, from one stock to another (e.g. the conversion of plant biomass into animal biomass). ***Parameters*** or ***converters*** are values of variables used to determine rates of flow. ***Connectors*** show the path through which material is transferred from one stock to another, or to and from sources and sinks. If a manager can accurately estimate the initial value of pertinent stocks, determine the conceptual framework (often, equations) that regulate the change in stocks or the rate at which stocks move or are converted to other ecosystem components, the values of the parameters, and the paths through which the stocks are transferred, then, components of interest in the ecosystem can be modeled. Take, as a highly simplified example, a system comprised of two stocks, populations of seaweed and their primary herbivore, limpets (a gastropod mollusk). An estimation of initial levels of these stocks, knowledge of values of six parameters (reproduction rates of limpets and seaweeds, the effect of limpet feeding on seaweed, limpet death rates, and density dependent constraints on limpet and seaweed population growth) and an understanding of connections between parameter values and rates of change in stocks (expressed in the equations) are sufficient to track changes in the populations (Figure 12.12) (Brennan et al. 1970).

Models that attempt to address all components of an ecosystem are much more complex than this simple example. However, models that make predictions about single effects or states may be much simpler. For example, in the Serengeti, Wolanski et al. (1999) conducted extensive field studies and hypothesized that water quality and quantity were the dominant forces driving ecological events. Background studies clearly established that the migration of ungulates was related to the level of rainfall and river flows, but these variables still did not predict animal movements with precision. Further investigations revealed that water quality, specifically salinity, was the most accurate predictor of ungulate movements. Where the water is fresh, wildlife remain. Where it becomes saline, they leave. Further, variation in salinity by decade was the most important factor determining the discontinuity between grasslands and wooded savannas. Modelers, using the value of average salinity from a single lake, were able to predict the movement of animals from grasslands to woodlands within 1 week when salinity values rose above a pre-determined threshold (Wolanski et al. 1999).

Modeling and monitoring are intimately connected because modeling identifies the critical ecosystem variables that are



Seaweed-limpet herbivory parameters:

Equations: $\Delta S/\Delta t = K_1 * S - K_2 * S^2 - K_3 * S * L$

$\Delta L/\Delta t = B * K_3 * S * L - K_4 * L - K_5 * L^2$

	Description	SIM1	SIM2	SIM3	SIM4
S	Seaweed biomass	100	100	100	100
L	Limpet biomass	10	10	10	10
K_1	Reproduction of seaweed	1.1	1.32	1.65	0.88
K_2	Seaweed density factor	1.0E-05	1.0E-05	1.0E-05	1.0E-05
K_3	Effect of limpet feeding	1.0E-3	1.0E-3	1.0E-3	1.0E-3
K_4	Limpet mortality	0.9	1.08	1.35	0.72
K_5	Limpet density factor	1.0E-4	1.0E-4	1.0E-4	1.0E-4
B	Limpet birth rate	0.02	0.24	0.3	0.16

FIGURE 12.12. Conceptual illustration, equations, parameter values, and simulation results (SIM1-SIM4) of a model of limpet herbivory on seaweed. Boxes (L and S) represent populations (stocks) of limpets and seaweed in the system. K1–K5 and B are parameters (constants) affecting rates of flow (dL/dt and dS/dt) between stocks and ecological sinks (clouds). (Equations and parameters derived from Brennan et al. 1970. Drawing by J. D. Schmeling.)

the best indices of changes in status or function of an ecosystem, and so make the monitoring effort more efficient and cost effective. By knowing what to sample and monitor, we eliminate the waste of time and money that could be spent monitoring variables that are *not* sensitive to ecosystem processes.

12.4.2. Fire

Ecological effects of fire vary, but in most ecosystems, fire can lead to increases in: (1) habitat heterogeneity and amount of edge; (2) plant and animal diversity; (3) nutrient uptake by plants, especially graminoids and forbs; (4) loss of nutrients from soil; (5) rates of erosion and surface runoff; (6) rates of streamflow; (7) grazing and browsing of burned areas by ungulates; and (8) establishment of early successional species (Knight and Wallace 1989; Leach and Givnish 1996; Van Dyke and Darragh 2006). All but the first of these effects are usually of short duration, generally lasting only 1–3 years. In contrast, increase in habitat heterogeneity may be a long-term effect, although its magnitude varies with the scale and intensity of fire. Small, dispersed fires tend to increase habitat heterogeneity, whereas large, contiguous fires make landscapes more homogeneous, particularly if the fire is hot and spreads rapidly.

Ecosystem managers can use fire to maintain or enhance biodiversity, increase habitat heterogeneity, increase plant nutrient uptake, create conditions attractive to particular species or other desired outcomes on a site-specific basis, or permit naturally ignited fires to burn over wider areas to create such effects through the ecosystem. In managing fire, managers can basically manipulate four variables. The first is the type of fire to be used. For example, managers could ignite a surface or a canopy fire in a forest, with each type producing radically different risks and results. The second manageable variable, closely related to fire type, is fire intensity. Managers can affect the amount of heat generated by a fire by their choice of site, the fuel types and accumulations that are present, and the environmental conditions under which the fire is set. Third, managers can and do manipulate fire frequency. For example, in North America, a tallgrass prairie burned every year will have a very different species composition and physical structure than one burned every 3 years, or every 5 years. Thus, management decisions about fire frequency will have important short-term effects on the species composition on burned sites, and potentially long term effects on landscape composition at larger scales. Finally, managers can alter fire timing, which is usually manifested in their choice of which season the fire is set. Again to use North American tallgrass prairies as an example, early spring fires ignited before germination of new, living plant biomass favor the establishment of a relatively small number of "warm season" grass species such as big bluestem, Indian grass, and switchgrass because the resulting bare, blackened soil readily absorbs large amounts of heat, increasing soil temperatures that favor germination of these and other species of grasses that germinate best in warmer soils. Summer burns, which burn living plants with higher moisture content and therefore burn less completely and intensely, tend to leave more plant material on the soil, reducing post-fire soil temperatures and favoring establishment of more diverse communities of "cool season" grasses and forbs.

Even if fire is allowed to burn without suppression throughout the system, it is unlikely to produce a stable pattern of landscape structure or to necessarily replicate previous historical landscape patterns (Baker 1989). Although site-specific application of fire can be beneficial, even essential, in fragmented habitats, the regional or ecosystem-wide use of prescribed fire is unlikely in the foreseeable future because of the lack of appropriate technology, insufficient financial and human resources in any one agency to control large-scale fires, and strong public and political opposition to large-scale fires as a management technique. Even the choice to allow fires to burn in relatively uninhabited ecosystems is problematic because large fires may spread to inhabited areas, resulting in loss of human life and property, and cannot be effectively controlled if they reach certain critical sizes. Although fire has been a powerful force in shaping ecosystems, its current applications in management will usually be limited to individual, relatively small sites.

12.4.3. Water Flow

Today most wetland and riparian systems are managed on a site-specific basis (Fredrickson 1997), but the processes that control them – most importantly, water flow – extend over vast areas. Although most lake systems remain relatively constant in water volume and flow, streams experience seasonal flow variations that significantly affect the stream ecosystem and associated terrestrial ecosystems. Variation in water flow is one of the most important determinants of ecosystem structure and function. Changes in water flow promote exchanges of nutrients among habitats and enhance system productivity. A flood pulse also can provide a dimension of "seasonality" to environments that are otherwise unseasonal, such as tropical rainforests, making them more productive and diverse (Sparks 1995). Systems that experience flow variations include some of the most species-rich places on earth, such as the Amazon rainforest, the papyrus marshes of the Nile, the swamps of the Okavango River in Botswana, and the shallow wetlands and lakes of the Gran Pantanal of the Paraguay River in South America. These areas also support important commercial fisheries (Welcomme 1985).

Natural flooding over a historical floodplain increases habitat heterogeneity during floods because differences in topography in the flood plain, even small depressions, will hold water longer and at greater depths, providing habitat for waterfowl, amphibians, and other terrestrial species that use ephemerally flooded areas. The recently developed technology of "laser leveling" (establishing a single slope across a field to provide irrigation to crops from floodwaters) eliminates small depressions and associated habitat heterogeneity (Fredrickson 1997), with predictable declines in species diversity.

Flooding lowers total biomass production over the short term, but usually does not have long-term effects. In the southeastern US, large, infrequent floods regulate the development of longleaf pine forests through differential mortality via complex interactions of forest landscape position, associated landforms, and sizes of individual trees. Infrequent but large-scale flooding can shift a population of trees from an uneven-aged stand to an even-aged one because the immediate post-flood period synchronizes germination of new individuals in the flooded area. Floods also move downed trees, limbs, and brush into stream channels, increasing channel structure, surface area, and roughness, promoting sediment retention, and increasing the stability of the channel surface. Such woody biomass in streams increases invertebrate activity, provides cover for fishes, and increases the habitat diversity of the stream channel (Michener et al. 1998).

Most stream species are adapted to flow variations, and decline in abundance if such variations are reduced or eliminated (Sparks 1995). Such species often use changes in flow as cues for seasonal breeding and feeding activity because optimal conditions for both are different and do not usually occur at the same time. If variations in flow rates cease, breeding and feeding activities may be curtailed or aborted. For example, in New Zealand, the endangered black stilt (*Himantopus novaezelandiae*) nests on gravel bars that are formed immediately after mountain snowmelt leads to spring floods. Dams that hold or divert water for agriculture change flooding schedules and submerge stilt nests (Boyce and Payne 1997). Similarly, the reduction in sand bar development in the Missouri River in the United States has reduced nesting habitat for the endangered piping plover (*Charadrius melodus*) and the more common least tern (*Sterna antillarum*).

In terms of human safety, property, and economics, floods are negative events. Thus, managers have tried to control or eliminate flooding through impoundments that reduce fluctuations in flow; to construct levees and other physical structures that reduce the size of the floodplain; and, on larger streams, to physically remove downed timber and other woody debris from stream channels to increase the ease, speed, and safety of navigation. In a context of ecosystem management, these are legitimate concerns. However, if floods are eliminated, flood-adapted components of the system will decline because flood pulses are the primary source of energy in many freshwater aquatic systems that facilitate habitat structure, nutrient exchange, and organism movement (Sparks 1995). Flooding also renews floodplain soil by depositing sediment and nutrients otherwise lost through erosion, depleted by crops, or sequestered in soil.

If flow is restricted to a narrower channel such that the floodplain cannot receive and store the floodwaters, flood heights and damages will increase at other locations. It is noteworthy that many dams on major rivers were built to aid navigation by maintaining river depth at a sufficiently high level during periods of lowest flow, not to stop floods (Sparks 1995). Under an ecosystem management approach, managers would not only manipulate flows of smaller streams in local watersheds, but larger dams also could be removed to restore natural flow regimes in larger watershed systems. Such actions are no longer conservation pipe dreams. A hydroelectric dam was destroyed in Maine (USA) to restore migration of Atlantic salmon, and the removal of several dams in the US Pacific Northwest is now being considered, as is a major dam in France (IUCN 2000).

12.4.4. Herbivory and Herbivores

Herbivores, especially large ones, often exert profound controlling influences on ecosystem components, structure and function. In many cases, ecosystem management is impossible without herbivore management, and the manager who fails to manage the ecosystem's herbivores often finds that the herbivores will manage the ecosystem for him, and not always to his intended ends. Herbivores affect ecosystem processes primarily through regulation of habitat, regulation of energy flow, regulation of plant nutrient cycling, and effects on plant nutrition. Both browsers (herbivores feeding on woody vegetation) and grazers (herbivores that feed on herbaceous vegetation) achieve these results, although not always through the same means.

Browsers often prevent the vertical development of sapling vegetation of their preferred food species, contributing to spreading, shrubby growth forms that keep the affected plant biomass within their reach (McNaughton et al. 1988). In northern boreal forests in Europe and North America, moose prevent saplings of preferred species from growing into the tree canopy, resulting in a forest with fewer canopy trees and a well-developed understory of shrubs and herbs, all within reach of the moose (McInnes et al. 1992)! In fact, light to moderate browsing leads to increased production efficiencies (higher rates of production per biomass) in shrubs and saplings that are browsed (Figure 12.13a). Through such browsing, moose also reduce the quantity and quality of litter and soil nutrients, driving a set of ecological interactions between browse, litter quality, and soil nutrients (McInnes et al.; Figure 12.14). Similar effects

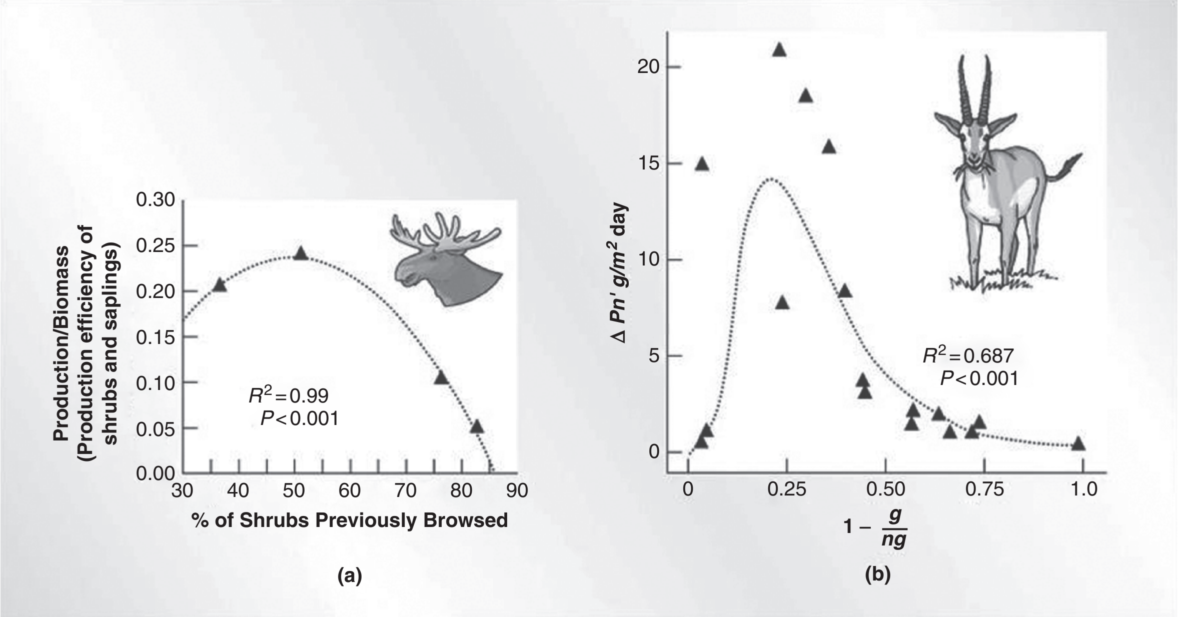


FIGURE 12.13. The relationship of browsing (a) and grazing (b) to production efficiency. In (a), light-to-moderate browsing by moose stimulates higher ratios of plant production per unit of biomass in shrubs. In (b), grazing produces a similar response function, with greatest increases in productivity (g/m^2/day) associated with intermediate levels of grazing intensity, 1 − *g/ng*. *g* is the biomass in grazed areas unprotected by fencing and *ng* is the biomass in a permanent exclosure in which no grazing occurs. (a) Courtesy of Ecological Society of America. (b) Grazing as an optimization process: grass-ungulate relationships in the Serengeti. S. J. McNaughton, *American Naturalist* 113:691–703, University of Chicago Press. Copyright 1979 University of Chicago.

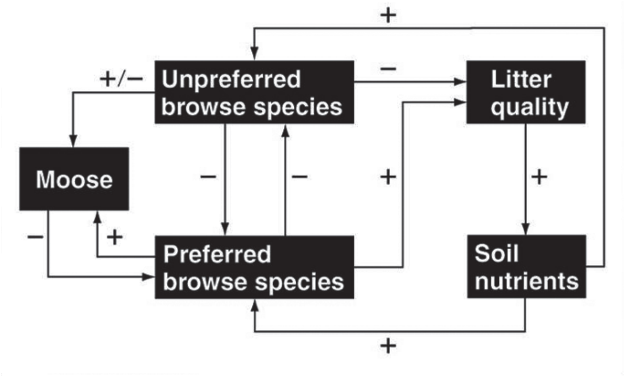


FIGURE 12.14. Relations between levels of moose browsing, preferred and unpreferred species of browse, litter quality, and soil nutrients. Arrows indicate direction of interaction. + signs indicate positive effects, − signs indicate negative effects. (Figure courtesy of Ecological Society of America.)

are seen in mixed deciduous-coniferous forests, where moose typically browse preferentially on deciduous hardwoods. This feeding pattern not only changes forest composition, but also reduces nitrogen mineralization, nitrogen inputs, and primary productivity of the forest because the browsing reduces the quantity and quality of litter returned to the soil (Pastor et al. 1993).

In Africa, mixed feeders that combine browsing and grazing, such as elephants (*Loxodonta africana*), regulate the abundance of woody browse and underlying grasses, often by pushing over trees or stripping their bark (McNaughton et al. 1988). These activities reduce the abundance of woody vegetation and create openings that grasses subsequently invade. A North American mixed feeder, elk, can, at high densities, suppress height and survivorship of trembling aspen and willow as well as a variety of conifer species through browsing (Chadde and Kay 1991; Kay and Wagner 1994; Romme et al. 1995). Similarly, white-tailed deer can reduce the survivorship of long-lived forbs, such as trillium, where most of the leaf area and reproductive structures can be removed in a single bite. Where deer densities are high and forest habitats are fragmented, there is experimental evidence that deer can extirpate trillium in individual fragments and inhibit efforts to later restore such populations (Augustine and Frelich 1998).

Grazing species affect a variety of components of ecosystem structure and function. In some systems, grazers can remove up to 40% of standing biomass, significantly reducing ecosystem production. In other systems, grazers may initiate changes in plant morphology and physiology that lead to higher levels of plant productivity. For example, in African grazed systems, dominant grasses are dwarfed, low growing forms with short internodes, while in ungrazed systems in the same area dominant grasses are tall growing species (McNaughton et al. 1988). When grazed, many plants respond by increasing biomass concentration in their tissues (the ratio of mass to volume, often measured in milligrams of plant biomass per cubic centimeters), creating more "biomass per bite" for herbivores. Gregarious herbivores exploit this response by actively creating "grazing lawns," intensely grazed areas within the ecosystem where the herbivores' own grazing activity keeps plant heights low and biomass concentration high. Although this reduces total plant biomass density in the grazing lawn compared to ungrazed areas, it increases foraging efficiency because of the increases generated in biomass concentration (McNaughton 1984). Grazing also tends to increase photosynthetic rates in plants, increase rates of nutrient allocation to growing plant tissues, increase growth rates in plants, and produce other effects that often benefit herbivores (Table 12.6). Light to moderate grazing by native herbivores produces positive responses in plants in growth rates, metabolic efficiency, and nutrient concentrations (McNaughton 1979). In fact, in an experimental analysis of grazed systems in the Serengeti-Mara regions of Tanzania and Kenya, McNaughton (1979) determined that over two-thirds ($r^2 = 0.69$) of variations in plant productivity could be explained by grazing intensity alone (Figure 12.13b), producing a response similar to that of browsing as previously discussed (Figure 12.13a).

Managers must not only consider effects of native herbivores, but also domestic livestock. For example, when livestock grazing is light or absent, grasses and sedges in upland Ponderosa pine (*Pinus ponderosa*) and mixed conifer forests of the US Rocky Mountains outcompete tree seedlings for space and nutrients. Tree density remains low and individual trees are large and widely spaced. When grazing is more intense, livestock reduce understory grasses and sedges, leading to increased survivorship and densities of trees, which some investigators assert leads

TABLE 12.6. A summary of important effects of herbivory on plant growth and metabolism.

Effects of Herbivory on Plants
1. Photosynthetic rates increase in the remaining tissue.
2. Older tissues, functioning at levels below maximum photosynthetic level, are removed.
3. The active photosynthetic period of residual tissue is prolonged as the rate of leaf senescence is reduced.
4. Substrates are circulated through the plant.
5. Removal of overshadowing tissue intensifies light on potentially more active underlying tissues.
6. Increased leaf growth and tillering result from the division and elongation of cells; the activation of remaining meristems increase due to the plant's hormonal response; and growth is also promoted by chemicals in ruminant saliva.
7. Transpiration surface is reduced. Consequently, soil moisture conservation increases.
8. Nutrients are recycled from dung and urine.

Source: Based on concepts from McNaughton (1979). Table design by M. J. Bigelow.

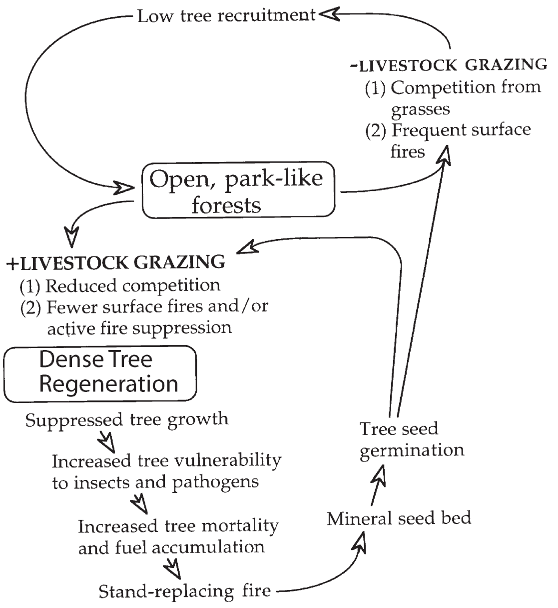


FIGURE 12.15. A conceptual model of the effects of livestock grazing on the stand dynamics of western, interior coniferous forests of the United States. Note that in the absence of livestock grazing, competition from grasses and sedges reduces survivorship of tree seedlings. Grasses and sedges also provide fuel for frequent, low intensity surface fires that also kill tree seedlings. Both effects lead to the production of low tree recruitment and low density, open, park-like forests. Livestock grazing removes grasses and sedges, leading to increased seedling recruitment and high density forests that can carry more intensive canopy fires. (Developed from concepts from Belsky and Blumenthal. Original figure by M. J. Bigelow.)

to more frequent and severe fires (Belsky and Blumenthal 1997; Figure 12.15). Livestock also reduce cover of herbaceous plants, increase soil disturbance and compaction, reduce water infiltration rates to soil, and increase rates of soil erosion (Belsky and Blumenthal 1997).

12.4.5. Predation and Predators

Although herbivores are predators on plants, we will use the term "predation" in this discussion in its more traditional sense of referring to acts of one animal killing another animal for food, and refer to animals that do it as predators or carnivores. Of all the factors in our short list, predation is perhaps the most variable in its effects on ecosystems and the most difficult to predict and control, but among the most important in ecosystem management. In some systems, predators can generate increases in biodiversity (Paine 1966, 1969), but this effect is not universal. Under most conditions large vertebrate carnivores, such as wolves, mountain lions, and bears, can regulate their own numbers through social interaction and behavior (Seidensticker et al. 1973; Beecham 1983; Fuller 1989). Carnivores can make functional (dietary shifts) and numerical (changes in density) responses to changes in prey abundance, but rarely do large carnivores actually regulate prey populations (Bergerud and Ballard 1988; McLaren and Peterson 1994). Even when regulation does occur, it is often short-lived or only during harsh conditions when prey are especially vulnerable.

Despite ambiguity about the importance of the role of predators in ecosystems, predation and predators, especially large vertebrate carnivores, are essential to consider in ecosystem management. Large vertebrate carnivores have the largest home areas of any group of terrestrial vertebrates. Thus, managers have traditionally believed that, if large carnivores were featured species of protection in ecosystem management, their large area needs would guarantee the survival of other species with smaller area needs that lived under the carnivore's "umbrella." Although intuitively appealing, this concept has never been carefully tested. One approximation is offered by Noss et al. (1996) who compared percentages of species protected in different taxa under two grizzly bear protection plans in Idaho (Shaffer 1992; US Fish and Wildlife Service 1993). Amphibian, bird, and mammal species were well protected under one or both plans, but reptile species distributions had little inclusion under either (Table 12.7).

Large predators also are driving forces in ecosystem management because their large dispersal distances force managers to consider the connectivity of regional ecosystems. The key question in such cases is, does there exist, or can there be made to exist, habitat corridors between adjacent ecosystems that large predators will use in dispersal and through which they can move with high rates of survivorship? The efficacy of corridors is still in need of better experimental study (Chapter 10), but observational and anecdotal evidence suggests that wide-ranging predators can use corridors, even those of apparently low habitat quality, to move from one regional ecosystem to another (Noss et al. 1996). The question of survivorship in corridors is not a matter of habitat characteristics and spatial considerations only, but also one of public attitude and education, which, in an ecosystem management approach, must be an important part of the management effort. Favorable public

TABLE 12.7. Comparison of the number of terrestrial vertebrate species with greater than 10% of their predicted statewide distribution protected by a recovery zone of a US Fish and Wildlife Service (USFWS) (1993) grizzly bear recovery plan and an alternative recovery plan (Shaffer 1992). Ubiquitous and peripheral species not included.

Class	State Total Species	USFWS Zones (%)	Alternative Zones (%)
Amphibians	8	4 (50)	5 (63)
Reptiles	13	0 (0)	2 (15)
Birds	126	66 (52)	100 (79)
Mammals	68	32 (47)	51 (75)
Total	215	102 (47)	158 (73)

Source: Noss et al., Conservation biology and carnivore conservation in the Rocky Mountains, *Conservation Biology*, Copyright 1996 by Blackwell Publishing.

attitudes toward predators tend to increase their densities, range, and persistence. Unfavorable public attitudes lead to their extermination. The presence of large predators brings national attention to the ecosystems in which they live, with attendant powerful national constituencies who act as the predators' advocates and can effectively exert political and social pressure on management decisions. However, no amount of advocacy for predators will change the fact that large predators are dangerous. They will kill livestock, pets, and, occasionally, humans. Their presence requires managers to devise multiple strategies for such control, or in some cases, eradication, in different contexts. For example, ***zonation management*** is one proposed method of managing wolves at an ecosystem level that would protect wolves in "core" protected areas but subject them to increasingly higher levels of control as populations move into areas with higher densities of livestock and humans (Mech 1995; Figure 12.16).

Managers may not always be able to easily manipulate predators and predation in an ecosystem management process, but the presence of large predators forces managers to expand their concern from local to regional interests, and to include political, sociological, and educational dimensions that encompass many stakeholder groups that otherwise might not be included in management decision making.

12.4.6. Managing Ecosystem Components, Structure and Function

Poiani et al. (2000) argue that an ecosystem can be considered "functional" if it (1) possesses the historic composition and structure of the ecosystem and its species within a natural range of variability; (2) has dominant environmental regimes controlled by natural processes; (3) is of sufficient size to possess at least one minimum dynamic area (50 times the size of the average disturbance patch); and (4) is connected to other essential landscape elements, among which species are free to move. But even if an ecosystem meets these criteria, how do we decide if it merits conservation priority?

Many conservation biologists would argue that this question is answered by an examination of endangerment. Is the ecosystem facing the threat of irreversible alteration, or are its species in danger of extinction? In this view, the best approach is to evaluate the ecosystem through attributes shared by endangered species. For example, Flather et al.

FIGURE 12.16. Zonation management for wolves or other large mobile predators. In a core protected area with low human densities and minimal human impacts, wolves receive complete protection. In a surrounding area (management area), wolf numbers are regulated and individual wolves that kill livestock or pets are destroyed. In surrounding areas of high human population densities and impacts, wolves are killed if they enter the area. (Based on a concept described by Mech (1995). Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reproduced with permission of the McGraw-Hill Companies.)

(1998) ranked counties in the United States, adjusted for size differences, by the number of threatened and endangered species in each, separated species groups by taxonomic units, and then identified areas where endangered species were concentrated as the top 5% for each group. A land resource classification system developed by the US Department of Agriculture arranged counties that had many endangered species into regions of similar climate, physiography, soil, vegetation, and land use. Each species was assigned an endangerment factor or factors that represented the reasons for its decline, and then a "factor diversity" index was calculated that represented the complexity of factors for that taxonomic group in that region. The larger the index value, the greater the complexity of endangerment factors and the more complex the recovery strategy needed (Flather et al. 1998). This method could provide an index of the distribution of endangered species and the complexity of the causes of their endangerment in any system, and help to identify where risks of extinction are concentrated. Flather et al.'s approach focuses on factors that affect many species and serves to prioritize management efforts because it identifies which species cover multiple areas and which are unique to particular areas, as well as identifying areas affected by few or many endangerment factors. Widely distributed species may respond to actions that change endangerment factors throughout the system more than species confined to smaller areas. Areas affected by few factors may be easier to protect with simpler management strategies than those affected by many factors. The method also could identify systems subject to greater endangerment stress (Flather et al. 1998).

12.5. What does Ecosystem Management Accomplish? The Fruits of Ecosystem Management Initiatives

12.5.1. Top-Down Approaches – Ecosystem Management Through Government Agency Initiative

Although still a relatively new concept, sufficient effort has been invested in ecosystem management approaches to permit some assessment of its efficacy and feasibility. Specifically, can conservation and resource management be done in the way it is envisioned, or, perhaps, idealized, in the ecosystem management paradigm? The answer to this question comes from examining case histories of *attempts* at ecosystem management and what actually happened as a result of these efforts.

One of the most comprehensive studies of ecosystem management implementation has been conducted by a team of conservation scientists led by Steven Yaffee of the School of Natural Resources and Environment at the University of Michigan (USA). Six hundred nineteen "candidate" projects were considered as efforts in ecosystem management, including initiatives from both government agencies and private conservation organizations. Of these, 105 were eventually selected for analysis based on how well the project met specified criteria for "ecosystem management," as well as providing regional and agency or group representation, and 103 of these were actually analyzed based on the responses of managers engaged in the projects. What did such efforts actually accomplish? The most common "outcomes of success" in such projects were improved communication and cooperation among agencies, organizations and stakeholders (74% of projects, Figure 12.17) and the actual development of a management plan (62%, Figure 12.17). Efforts were least successful in educating the public about the management plan (19%), changing management practices (19%), increasing scientific understanding (15%), or increasing trust among stakeholders (14%) (Yaffee et al. 1996). Paralleling these outcomes, factors that contributed most to project success were collaboration (61%) and public support (59%) (Figure 12.18) (Yaffee et al. 1996).

The US Forest Service has attempted to operationalize ecosystem management into six assessable goals: (1) improved collaboration in decision making; (2) integration of multiple sources of scientific information; (3) integration of multiple sources of social and economic information; (4) adaptive management and monitoring of ecosystem conditions; (5) improved inter-agency cooperation; and (6) preservation of ecological processes and promotion of ecological sustainability. To evaluate the agency's per-

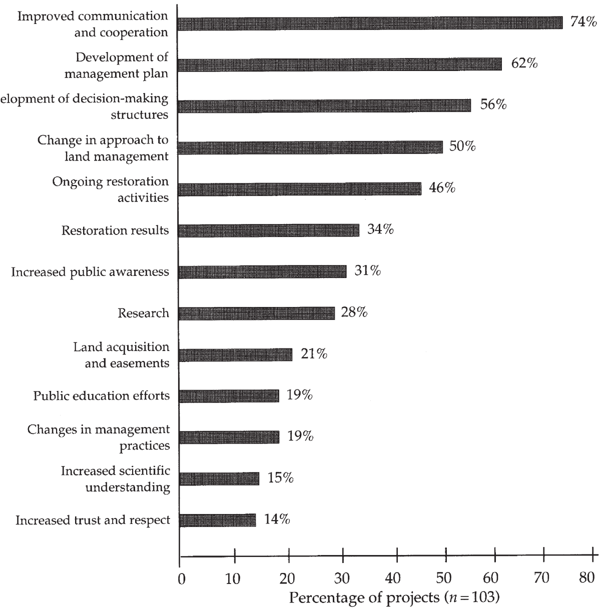


FIGURE 12.17. Outcomes (%) of 103 ecosystem management projects initiated in the United States from 1994 to 1996. (From *Ecosystem Management in the United States* by Steven L. Yaffee et al. Copyright 1996 by The Wilderness Society. Reproduced by permission of Island Press, Washington, DC.)

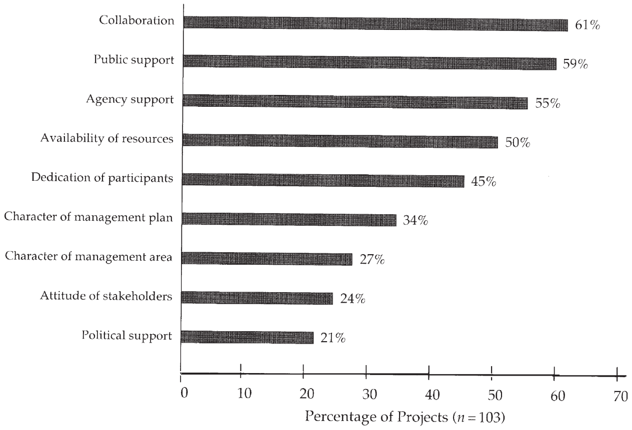


FIGURE 12.18. Factors (%) that contributed to facilitation and progress of 103 ecosystem management projects initiated in the United States from 1994 to1996. (From *Ecosystem Management in the United States* by Steven L. Yaffee et al. Copyright 1996 by The Wilderness Society. Reproduced by permission of Island Press, Washington, DC.)

formance, resource scientists Kelly Butler and Tomas Koontz engaged in Forest Service document analysis, interviews, and surveys of 345 Forest Service managers that included district rangers, supervisors of national forests, and regional foresters from all national forests in every region. Specifically, Butler and Koontz examined how well managers perceived these goals had been implemented in actual agency procedures. Overall, managers felt they had greatest success in improving collaboration and integrating multiple sources of scientific information under an ecosystem management approach (Butler and Koontz 2005), paralleling Yaffee et al.'s finding that "improved communication" was the most frequently achieved success in ecosystem management projects. Managers reported least success in implementing adaptive management (Butler and Koontz 2005), matching Yaffee et al.'s finding that ecosystem management approaches seldom changed current practices or led to the discovery of new scientific information. Forest managers attributed this failure to the difficulty of making changes in established procedures required by adaptive management, the high cost of monitoring, and lack of public support for such efforts (Butler and Koontz 2005).

12.5.2. Initiative from the Bottom-Up – Emerging Coalitions Driven by Environmental Concern

A recurring problem in implementing ecosystem management based on the initiatives of government agencies is that this approach requires the creation of permanent committees, boards, or working groups in which all agencies with jurisdiction or interest in the ecosystem are represented. Unfortunately, many attempts at ecosystem management by government agencies simply create *ad interim* groups for individual ecosystem management projects and fail to form the kinds of genuine "partnerships" defined earlier that are essential for success. To be effective in the long-run, ecosystem management groups would not only need to be like such previously described partnerships, but also be more-or-less permanent, have their own budgets, and possess the authority, especially through inclusion of legal and political mechanisms, to make meaningful decisions about ecosystem management policies.

Such sweeping organizational changes are difficult for agencies to make. However, examples of radical re-organization and partnership have begun to emerge from citizen-based initiatives, especially in the form of "watershed councils" which consist of groups of public and private stakeholders that address ecosystem needs within individual watersheds. For example, the US Pacific Rivers Council funded a comprehensive study of Pacific salmon populations in the US Pacific Northwest that produced methods and guidelines for prioritizing these populations for conservation (Allendorf et al. 1997). A more comprehensive initiative in privately-led environmental management efforts, also using watersheds as the fundamental ecosystem management unit, has emerged in Hawaii (USA). On the Hawaiian Islands, upland forest watersheds are of significant value as reservoirs of biological diversity, recharge areas critical for underground aquifers, and sources of billions of gallons of surface water to agricultural, residential and commercial sectors. However, the Hawaiian rain forest has been significantly degraded and reduced to only 58% of its original cover, and continues to be under pressure from development, increasing demand for water, and continued environmental degradation caused by feral and invasive alien species. State government agencies lack sufficient resources to address comprehensive ecosystem management of these watersheds because of minimal investment for forest protection at the state level. In addition, much remaining forested landscape is in the hands of private landowners. In this situation, private landowners, non-governmental organizations, and state and federal agencies in Hawaii have formed partnerships to conserve and manage the state's forested watersheds by voicing their concerns, generating and implementing action plans and petitioning for greater support (Gutrich et al. 2005).

The first such collaboration to attempt an ecosystem management effort in Hawaii was the East Maui Watershed Partnership. In this case, stakeholders wanted to establish long-term protection of forests in the watershed by placing a fence around the watershed to exclude feral ungulates (mainly pigs and goats) from higher elevations, remove pigs and goats already in the forest by hunting and trapping, and remove or slow the spread of exotic plant species. Other partnerships with similar objectives soon began to develop in other watersheds, supported by the Hawaii State Legislature's declaration of 2003 as the "Year of the Hawaiian

Forest," a move that brought attention, and some funding, to forest ecosystem management and protection initiatives. In this effort, watershed partnerships established a pattern of building effective collaboration and management (Figure 12.19) based on a recurring set of common principles and procedures. First, participants found that using interdisciplinary science-based models to identify management targets and strategies was most effective. Informed by such models, participants gained a shared and accurate view of the state of the system and the processes driving it, and developed a common understanding of threats facing the system. Note that this strategy illustrates in practice what was described earlier in principle; the use of conceptual models as heuristic devices to improve communication among people of diverse backgrounds and expertise.

Second, effective partnerships developed a common language among stakeholders and decision makers for comparing various management options that were proposed. This occurred through repeated and iterative stages of scientific analysis that informed stakeholder deliberations, and such deliberation in turn directed subsequent analysis.

A third requisite was trust, which consistently proved an essential element to building consensus. Watershed coalitions found that, to build trust, the integration of scientific input needed to be transparent and responsive to feedback from the public. Public trust of scientists was high when scientists were viewed as independent and objective, but low when scientists were perceived as members of a coalition with a pre-determined agenda. In general, when government officials established high levels of trust among non-government stakeholders, stakeholders were willing to accept agency analyses with little reservation or debate. If trust was low, stakeholders demanded independent analysis and took longer to reach agreement on management plans. Invariably, when trust was absent, it undermined effective application of scientific input. In the absence of trust, no consensus was achieved and partnerships failed.

Fourth, watershed partnerships had to give careful consideration to the actual benefits and costs accrued to each stakeholder group under different management options. Plans that called for substantial costs to be borne by stakeholders who had been excluded from the planning process were the least likely to succeed (Gutrich et al. 2005).

Finally, a commitment to repeated, deliberative, dynamic discussion and decision-making processes increased the probability of achieving consensus among stakeholders. The more discussion and deliberation fostered communication, the more it increased the level of common understanding, shared values and vision, and mutual trust and respect. Deliberations also needed to be repeated and iterative, allowing not just for the presentation of information *to* stakeholders, but the processing of information *by* stakeholders (Gutrich et al. 2005).

There are cases in which unique circumstances force both agencies and citizens to consider new approaches to problems that resist solution by traditional methods. The

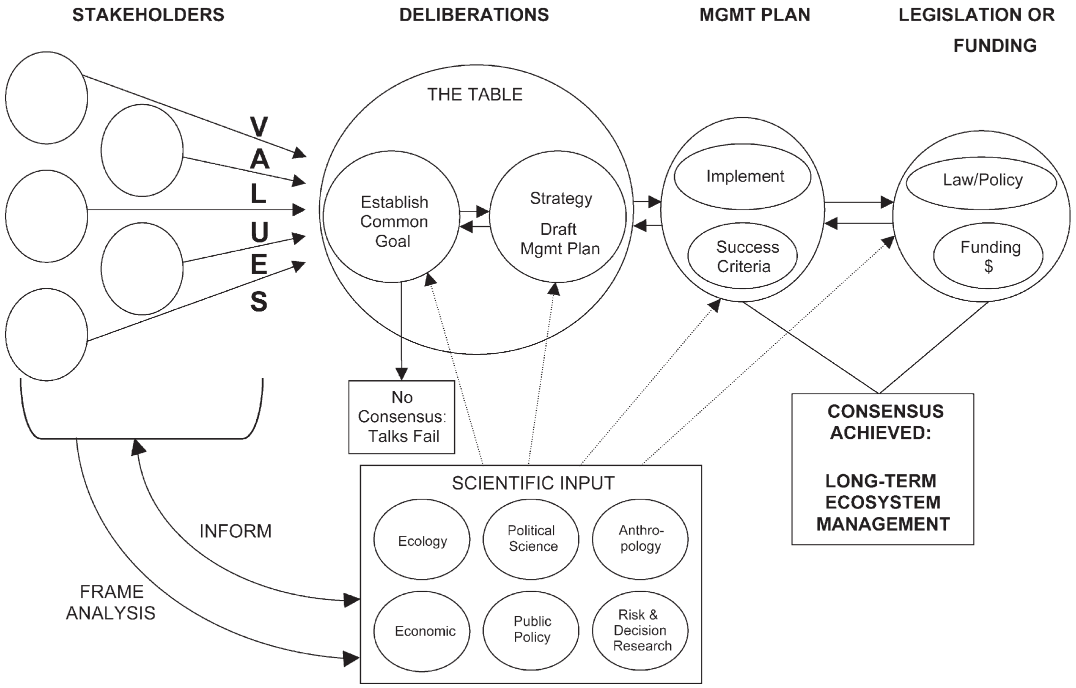


FIGURE 12.19. A general framework of the public process for building partnerships, achieving consensus, and implementing management plans among public and private stakeholders as employed in watershed partnerships in Hawaii (USA). (Gutrich et al. 2005. Copyright 2005. With permission from Elsevier.)

northern spotted owl offers a case history that reflects one of the earliest efforts to initiate an ecosystem management approach in conservation, and also reveals why such an approach may be needed to define, understand and solve problems that superficially appear to be only issues of single-species management.

12.6. Why Ecosystem Management Matters – The Case of the Spotted Owl

As recently as the late 1960s, little was known about the uncommon and rarely seen northern spotted owl (Figure 12.20), which inhabits the US Pacific Northwest. In the summer of 1967 Eric Forsman, an undergraduate student at Oregon State University (OSU), learned that he could usually elicit the owl's response if it was present by imitating its call (Meslow 1993). When Forsman and a fellow undergraduate, Richard Reynolds, began to use this technique to search for spotted owls in Oregon, they discovered that the birds could regularly be found in old-growth forests, but rarely in other habitats. Forsman and Reynolds brought their data to the attention of OSU professor Howard Wight. Wight was interested, and by 1972, Forsman had begun graduate research on the spotted owl under Wight's direction (Meslow 1993).

FIGURE 12.20. The northern spotted owl (*Strix occidentalis caurina*), a species that can only be effectively preserved with an ecosystem management approach to its obligate habitat, old growth conifer forests. (Photo courtesy of US Forest Service.)

Forsman's studies of the spotted owl revealed a pattern of habitat use and population distribution in conflict with management policies of the US Forest Service (Forsman et al. 1984). Managers viewed the owls' preferred habitat of old-growth forests as areas of low productivity (individual trees were no longer adding significant annual biomass), with many trees near the end of their life span ("overmature stands"). From this perspective, the rational management policy was to cut old-growth timber. Timber management policy on US public lands, however, operates within a context of environmental law, and two laws enacted during the studies of the spotted owl had significant effects on this management plan.

In 1973, the US Fish and Wildlife Service (FWS) included the spotted owl in its "Red Book," an early version of the official US list of endangered species. At the same time, interest in the conservation of old-growth forests was increasing. After the owl's Red Book listing, an appointed interagency group, the Oregon Endangered Species Task Force, recommended that management agencies retain 300 acres of old-growth forest around every spotted owl nest site (Caldwell et al. 1994). This recommendation was rejected by the Forest Service and the US Bureau of Land Management (BLM) because both agencies wanted a statewide population management goal established for spotted owls before implementing site specific management practices (Meslow 1993). However, when the US Endangered Species Act (ESA) became law later in 1973, the northern spotted owl was not listed as an endangered species, and its omission seemed to resolve the controversy. In reality, the conflict was just beginning.

In 1976, the newly enacted National Forest Management Act (NFMA) directed the Forest Service to "maintain viable populations of existing native and desired non-native vertebrate species" on national forests (Wilcove 1993). In other words, the NFMA and its attendant policies told the Forest Service that it was not allowed to create any more endangered species, nor was it allowed to destroy portions of a species' range or habitat (Meslow 1993). Although the concepts and techniques of population viability analysis were still in their infancy, it was clear that the initial recommendation of 300 acres for each pair of owls was inadequate because the protection of such small areas would not protect enough individuals to sustain the population (Wilcove 1993). The Oregon Endangered Species Task Force then recommended a goal of maintaining 400 pairs of spotted owls on public lands in Oregon. The plan called for protecting habitat in ways that would provide for clusters of three to six pairs of spotted owls, although single-site management was still permitted. Core areas for clustered pairs were to be no more than 1.6 km apart and each pair was to have a core area of 300 acres. Subsequent studies on radio-tracked owls (Forsman 1980; Forsman and

Meslow 1985) demonstrated that individual owls needed at least 1,000 acres, not 300 acres, of old-growth forest for permanent territories. In light of this data, the spotted owl management plan was revised and recommendations were changed to 1,000 acres of old-growth forest for each pair of owls within 1.5 miles of their nest site. However, the recommendations were rejected by the BLM and only partially followed by the Forest Service (Meslow 1993).

A population viability analysis by Russell Lande concluded that the spotted owl population was declining, and that the population could not be conserved unless significant portions of the landscape remained in old-growth forests (Wilcove 1993). In subsequent analyses, Lande concluded that the population was stable under current conditions, but refined his model to estimate the probability of population persistence at differing levels of habitat loss (Lande 1988). Based on this analysis, Lande determined that the spotted owl population could not persist with less than 20% of the landscape in old-growth forests. In contrast, the Forest Service proposed management guidelines that would conserve only 6% of the landscape in old-growth forests (Wilcove 1993). The Seattle Audubon Society sued the Forest Service for failing to adopt a credible conservation strategy in compliance with NFMA, eventually gaining an injunction against 135 timber sales in spotted owl habitat (Caldwell et al. 1994). In the midst of these controversies, the FWS was petitioned again in 1987 to list the spotted owl as an endangered species under the ESA. The FWS claimed the listing was unwarranted, but in 1988 a coalition of conservation groups filed an appeal against the agency's decision in Federal Court. In his judgment regarding the case, *Northern Spotted Owl v. Hodel*, Judge Thomas Zilly wrote that "The [Forest] Service disregarded all the expert opinion on population viability, including that of its own expert, that the owl is facing extinction, and instead merely asserted its expertise in support of its conclusions." Zilly ordered the Fish and Wildlife Service to reconsider its decision against listing the owl as threatened or endangered (Gordon and Lyons 1997).

By 1989 the successful litigation by the Seattle Audubon Society led Forest Service Chief Dale Robertson to appoint an Interagency Scientific Committee (ISC) to "develop a scientifically credible conservation strategy for the northern spotted owl" (Meslow 1993). The ISC recommended a strategy that called for a system of habitat conservation areas (HCAs) on public forest land in Washington, Oregon, and California (Thomas et al. 1990). In Washington and Oregon, each HCA would accommodate 20 pairs of owls, spaced at 19 km intervals. In California, where old-growth forests are more fragmented, HCAs were to accommodate at least ten pairs of owls and be no more than 10 km apart (Harrison et al. 1992). No timber harvesting would be allowed in the HCAs (Caldwell et al. 1994), and the "50-11-40" rule provided for dispersal of juvenile owls from one HCA to another by requiring a certain amount of landscape timber coverage (50%) of acceptable size (at least 11 in. diameter) and associated canopy closure (40%) in each quarter township in areas lying between adjacent HCAs (Harrison et al. 1992; Franklin 1993; Meslow 1993; Wilcove 1993). The new plan protected 7.7 million acres of forests, with 30% of the landscape preserved in old-growth forests. The strategy also allowed about 500,000 acres of old-growth forest outside of HCAs to be cut (Harrison et al. 1992). Concurrent with these recommendations, the FWS re-examined the status of the spotted owl in 1989 and proposed listing it as a threatened species (Wilcove 1993). By 1990, the owl was officially listed.

The ISC strategy was the subject of more lawsuits against the Forest Service in 1991 that prevented it from selling timber under the new plan. Eventually, US District Judge William Dwyer ruled that the plan carried significant risks to the owl and that the Forest Service had failed to consider the needs of other species in old-growth forests (Harrison et al. 1992). In the meantime, Congress commissioned its own investigation and assessment committee, the Scientific Panel on Late-Successional Forest Ecosystems, a group which came to be known simply as "The Panel" or "The Gang of Four." The Panel developed 14 management alternatives for congressional consideration, each of which was regional in scope, ecosystem-based in management, and risk-driven relative to the survival of the owl. Some were considered in proposed legislation, but none made it to a vote or were included in enacted legislation (Gordon and Lyons 1997).

Although an apparent failure at the time, The Panel made a valuable contribution to the development of ecosystem management by demonstrating to those involved in the political process that a biologically sound solution did not simply require a different management plan, but a fundamental change in traditional forest management practices. All 14 management alternatives are now recognized as early models of ecosystem management approaches, each offering management strategies that broke from the traditional resource management strategy of limiting or eliminating management from specific areas of the forest ("preserves") and permitting intensive management in others ("timber sales"). Serious consideration of these alternatives also changed the political debate from being about forest acres reserved versus board feet to a discussion about how to prevent multiple species management problems by integrating management across the entire forest landscape at regional levels (Gordon and Lyons 1997). It was not surprising, given his agency's experience with the northern spotted owl, that Forest Service Chief Dale Robertson announced, in 1992, that his agency would begin taking an "ecosystem approach" to all subsequent forest management plans, a date we noted at the beginning of this chapter as the "birthday" of ecosystem management in the United States.

Had the Forest Service been permitted and legally empowered to function according to its traditional bureaucratic organizational methods, it is quite possible that the spotted owl might have been exterminated. In this case, the driving force for the shift to an ecosystem level approach was outside input from citizens, the scientific community, and other agencies, all essential elements in the implementation of ecosystem management. Implementation of the plan led to reductions in timber harvests and loss of jobs in some parts of the timber industry in the Pacific Northwest, creating local antagonism against the spotted owl at least as passionate as that of its support in the conservation community. Despite its missteps and imperfect solutions, the development of the forest management plan for the northern spotted owl remains a watershed event in the emergence of ecosystem management as a comprehensive conservation strategy. This case irrevocably shifted management emphasis from individual sites to functional ecosystems, and its resulting recommendations have been incorporated into many subsequent studies of old-growth forests and their management (Wilcove 1993). The story of the spotted owl permits us to track the evolution of management strategy from resource management to ecosystem management, and at an early stage in the development of this paradigm shift. Note the progression in management focus and strategies for the owl.

Individual pairs
↓
Small isolated clusters of pairs
↓
Small clusters of pairs arranged in a habitat network (spatial structure)
↓
Large clusters of pairs connected by landscape habitat corridors (spatial structure with connectivity)

As population management strategies changed over time with the spotted owl, so did management of its surrounding environment. Conceptually, that progression was:

Site-specific protection of small habitat units
↓
Protection of clustered habitat units
↓
Protection of a network of habitat around clusters
↓
Protection of an ecosystem (old-growth forests) as a specific percentage of landscape

This story also illustrates the scientific, social, legal, and political elements necessary for ecosystem management to succeed:

Scientific research establishes conservation concern
↓
Concern is connected to agency management practices
↓
Agency management practices are affected by legislation, public input, and judicial review
↓
Judicial review forces interagency cooperation to achieve compliance
↓
Interagency cooperation increases inclusiveness in decision-making and requirements for empirical data and scientific reliability
↓
Increased inclusiveness and reliability strengthens support for management proposals

POINTS OF ENGAGEMENT– QUESTION 3

What elements of the spotted owl's demographics and habitat preferences created anomalies that a resource management approach was unable to solve? What features of an ecosystem management approach were better suited to address these same problems?

12.7. Synthesis

Ecosystem management, like any form of conservation management, should be undertaken with caution and humility. It is sobering to study the findings of ecologist C. S. Holling, who determined, after an examination of 23 managed ecosystems, that it was management activities that led to the collapse of these systems (Holling 1995). In order to work, ecosystem management must have a scientific basis that can identify what kinds of questions to ask, what data to collect and how to collect them, how to model the system to be managed, and how to create adaptive management mechanisms that are responsive to changing ecosystem needs and human concerns. It also must have goals aimed at ecosystem persistence, not commodity production.

Ecosystem management has become necessary and urgent in many contexts because of the failure to address current conservation problems under more restrictive approaches that quickly exhaust too much conservation effort on too few species, even as they overlook biota that are small, difficult to classify, or not appealing to public sentiments. But ecosystem management remains technically and politically challenging. To make progress, conservationists must develop a common, accepted, and operational definition of the concept, devise practical ways to implement it under varying conditions, and create political support and legislative mandates to translate ecosystem management concepts into enforced policy directives. Progress will necessitate conflict and clarification of values. Individual agency jurisdictions must be replaced with permanent working groups or boards with independent budgets, regional authority, and legal mandates. Without these, ecosystem management will remain a compelling theoretical concept, but a frustrating and unfulfilled practice.

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13

Conservation Economics

[What] seems to be wealth may in verity be only the gilded index of far reaching ruin …

John Ruskin (1883)

In this chapter you will learn about:

1. **The role of economics in conservation theory and practice**
2. **Economic processes and strategies that can contribute to environmental protection and conservation**
3. **Integrated approaches to economic development and biodiversity conservation**

13.1. Identifying and Protecting the Values of Biodiversity

13.1.1. The Value of Ecosystem Goods and Services

Economic behavior is arguably the most accurate expression of national, corporate, community, and individual values. No conservation effort can long endure without intimate connection to value. And no expression of value in conservation can endure with vitality unless it finds expression in economic behavior, either through what we spend to acquire what is needed by other species, or what we do without in order that what is needed by other species is not consumed and destroyed. People give generously to conservation because they value the ends its seeks to achieve, but the very money they give comes from economic processes that degrade the biodiversity they are seeking to protect. Trauger et al., after completing a technical review for The Wildlife Society on the relationship between economic growth and wildlife conservation, noted that there exists “a fundamental conflict between economic growth and wildlife conservation” (Trauger et al. 2003:2). But what is the nature of this conflict and why does it exist?

To accomplish its ends, conservation needs money, and large amounts of it come from people who have sufficient affluence to give to charitable causes, of which they perceive conservation to be one. For example, in Canada, Yen et al. (1997) surveyed three Canadian provinces to determine the variables affecting contributions to conservation. Income had the largest effect on the probability and amount of donation. In the United States, Pergams et al. (2004) found that stock market indices, such as the Dow Jones Industrial Average and the Standard & Poor’s 500 Index, gross domestic product (GDP), and personal income (PI) explained as much as 99% of annual variation in total revenue (including contributions) to four of conservation’s largest nongovernmental organizations (NGOs), the World Wildlife Fund, Sierra Club, Environmental Defense Fund, and The Nature Conservancy. These broad economic indicators also explained as much as 96% of the annual number of university conservation programs, 83% of membership in professional conservation organizations (Natural Areas Association, Society for Conservation Biology), and 93% of national park visitation. Commenting on these extraordinarily high correlations between economic growth and conservation funding, these investigators noted, “The conservation activity parameters we measured may exhibit positive trends even in the face of declining biodiversity, but biodiversity conservation will ultimately require the cessation of economic growth. The challenge to the conservation biology community is to retain a significant presence during and after the cessation of growth” (Pergams et al. 2004:1617).

This tension that exists between generating financial resources for biodiversity conservation and the wealth-generating processes that represent some of the fundamental causes of biodiversity loss is one of many of the basic tensions between conservation and the economy. Directly or indirectly, humans appropriate resources at the expense of other living creatures; indeed, the resources taken often *are* the living creatures. Yet the conservation of genetic diversity, populations, habitats, landscapes, and ecosystems will require that humans find ways to use resources that do not degrade or destroy them. Conservation biologists must explicate the relationships between human consumption and the persistence of other living creatures, and identify ways of changing patterns of human population growth and resource consumption to achieve conservation goals.

A healthy environment is the basis for maintaining the biodiversity of the natural world. And one of the most basic and generalizable expressions of the relationships between the economy and the environment is the so-called ***Ehrlich Identity***, formalized by biologists Paul and Anne Ehrlich (Ehrlich and Ehrlich 1990) as

$$I = P \times A \times T$$

where I is environmental impact, P is population, A is affluence (a measure of consumption), and T is technology (an index of efficiency of resource use and pollution abatement). The identity is of little value mathematically (for one thing, it is very difficult to express I in meaningful units or find common units for all the variables), but it is useful conceptually. The Ehrlich Identity asserts that environmental impact is not simply a function of human population density, but also of per capita consumption (A) and efficiency of resource use (T). Furthermore, the relationship between impact and other variables is complex and often non-linear. For example, extreme poverty (very low values of A) often results in great environmental damage because of the direct and destructive manner in which impoverished peoples obtain resources, but environmental damage of some forms may actually decrease as people become more affluent. This relationship is displayed graphically in a family of expressions generally known as ***Environmental Kuznets Curves*** (EKC). Originally developed as an expression of the economist Simon Kuznets theory that economic inequality increases over time, and then at a critical point begins to decrease (“Kuznets’ hypothesis”) (Kuznets 1955), the basic inverted u-shaped Kuznets Curve was increasingly adapted to environmental economics and policy as a way of relating environmental quality to income levels, beginning in 1991 when economists G. M. Grossman and A. B. Krueger noted the appearance of Kuznets Curve in their analysis of the potential environmental impacts of the North American Free Trade Agreement (NAFTA). From this point on, Kuznets Curve has been used to show how specific measurements of environmental quality, such as sulfur dioxide and particulates in the air (an index of one kind of air pollution) will at first increase with a population's per capita income (an index of its affluence) but, at some critical point, begin to decrease as per capita income rises further (Figure 13.1).

Indirectly, Kuznets Curve is a simple and general expression about the relationship between wealth and environmental quality. But its happy result (the richer you are, the less environmental damage you will do) holds only in specific settings and populations, and only in those cases because it does not consider some of the additional costs of affluence to ecosystems. Some have argued that the many Kuznets Curves for individual variables are a result of trade patterns, especially those in which affluent countries shift their heaviest polluting industries to less developed countries, a practice known among environmental economists as "environmental dumping."

The problem of externalities in environmental economic analysis is one that we will return to later in greater detail, and one in which the relationship between affluence and pollution may be more complex than the Kuznets Curve first makes it appear. Like the Kuznets Curve, the Ehrlich Identity also offers a simple, if somewhat different, way of expressing the relationship between people and the things the environment provides for them, that array of values that many economists call "ecosystem services." Ecosystem services refer to particular ecosystem functions that have value to humans. Consider the services of a single ecosystem, a forest (Table 13.1). As you read this list, consider how many of these services you actually think about paying for. If your honest answer is few or none, you are not alone. Throughout history, humans have lived depending on these services, but routinely taking them for granted. These services were simply expressions of "the way Nature works." But there are other ecosystems besides forests. Consider the scope of ecosystem services with less depth but more breadth, as displayed in Figure 13.2. In every ecosystem the combination of services produced is unique, but invariably valuable, indeed, essential to our well being. Sadly, we can no longer take such services for granted today. In the most comprehensive survey of ecosystem services ever made, the 1,360 scientists who compiled the World Resources Institute's *Millenium Ecosystem Assessment* (MA) in 2005 found that, of 24 ecosystem services examined worldwide, 15 (60%) were being degraded or used unsustainably. Only four have seen their capacities enhanced during the past 50 years (MA 2005) (Table 13.2). Ecosystem services are becoming scarce resources for which we will have to pay higher prices. As ecosystems and the services they provide are degraded, global biodiversity is diminished.

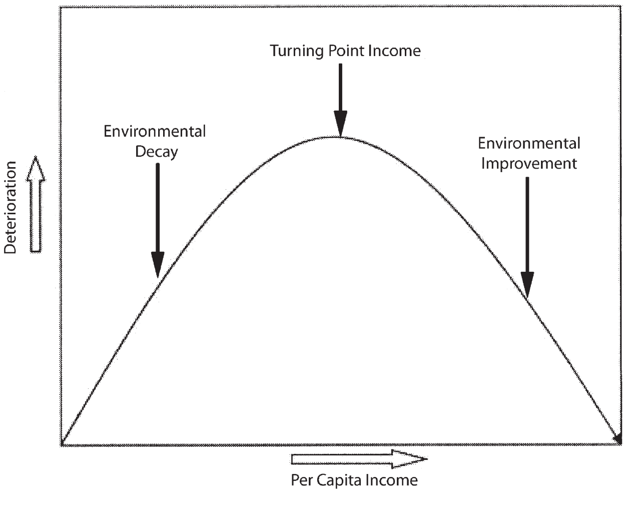

FIGURE 13.1. A generalized version of an Environmental Kuznets Curve (EKC) in which environmental deterioration first increases with increasing per capita income, but then decreases as income passes some critical point. EKCs often appear in relationships between particular environmental indices and specific human populations, but the relationship generally does not hold at regional or global scales. (Drawing by M. J. Bigelow.)

13.1.2. Stock-Flow Resources and Fund-Service Resources

We can further clarify our thinking about the economic value of biodiversity, and the ecosystems in which it resides, by realizing that such economic value is manifested in tangible *goods* (material resources) and *services* (functions of value to us performed by some other entity). The material goods we use and derive from ecosystems and their associated biodiversity are marvelously diverse, but all of these resources can logically be placed in one of two categories. ***Stock-flow resources*** are goods that are produced through a transformation process that occurs in the ecosystem itself, and which are normally self-renewing. Goods in this category are produced from a standing crop or "stock" of a resource that is transformed in some form of long- or short-term ecological process into a new kind of material, which can then be taken or extracted for use at a certain rate or "flow." For example, timber from a forest ecosystem is a stock-flow resource in which a standing crop or stock of mature trees transforms water, sunlight, and nutrients from the soil into new biomass (the trees get bigger) and new individuals (seeds that germinate into new, albeit much smaller, trees). If a stock-flow resource is harvested or extracted at a rate less than or equal to the rate of its renewal process, it is self-perpetuating. That is, we can manage such a resource

Table 13.1. Some examples of ecosystem services provided by a forest.

Ecosystem Service	Examples from Forests
Gas regulation	Trees store CO_2 and growing trees create O_2; forests can clean SO_2 from the atmosphere.
Climate regulation	Greenhouse gas regulation; evapotranspiration and subsequent transport of stored heat energy to other regions by wind; evapotranspiration, cloud formation, and local rainfall, effects of shade and insulation on local humidity and temperature extremes.
Disturbance regulation	Storm protection, flood control (see water regulation), drought recovery, and other aspects of habitat response to environmental variability mainly controlled by vegetation structure.
Water regulation	Tree roots aerate soil, allowing it to absorb water during rains and release it during dry times, reducing risk and severity of both droughts and floods.
Water supply	Evapotranspiration can increase local rainfall; forests can reduce erosion and hold stream banks in place, preventing siltation of in-stream springs and increasing water flow.
Waste absorption capacity	Forests can absorb large amounts of organic waste, and filter pollutants from runoff; some plants absorb heavy metals.
Erosion control and sediment retention	Trees hold soil in place, forest canopies diminish impact of torrential rainstorms on soils, diminish wind erosion.
Soil formation	Tree roots grind rocks; decaying vegetation adds organic matter.
Nutrient cycling	Tropical forests are characterized by rapid assimilation of decayed material, allowing little time for nutrients to run off into streams and be flushed from the system.
Pollination	Forests harbor insects necessary for fertilizing wild and domestic species.
Biological control	Insect species harbored by forests prey on insect pests.
Refugia or habitat	Forests provide habitat for migratory and resident species, create conditions essential for reproduction of many of the species they contain.
Genetic resources	Forests are sources for unique biological materials and products, such as medicines, genes for resistance to plant pathogens and crop pests, ornamental species.
Recreation	Eco-tourism, hiking, biking, etc.
Cultural	Aesthetic, artistic, educational, spiritual and/or scientific values of forest ecosystems.

Source: Table format by M. J. Bigelow.

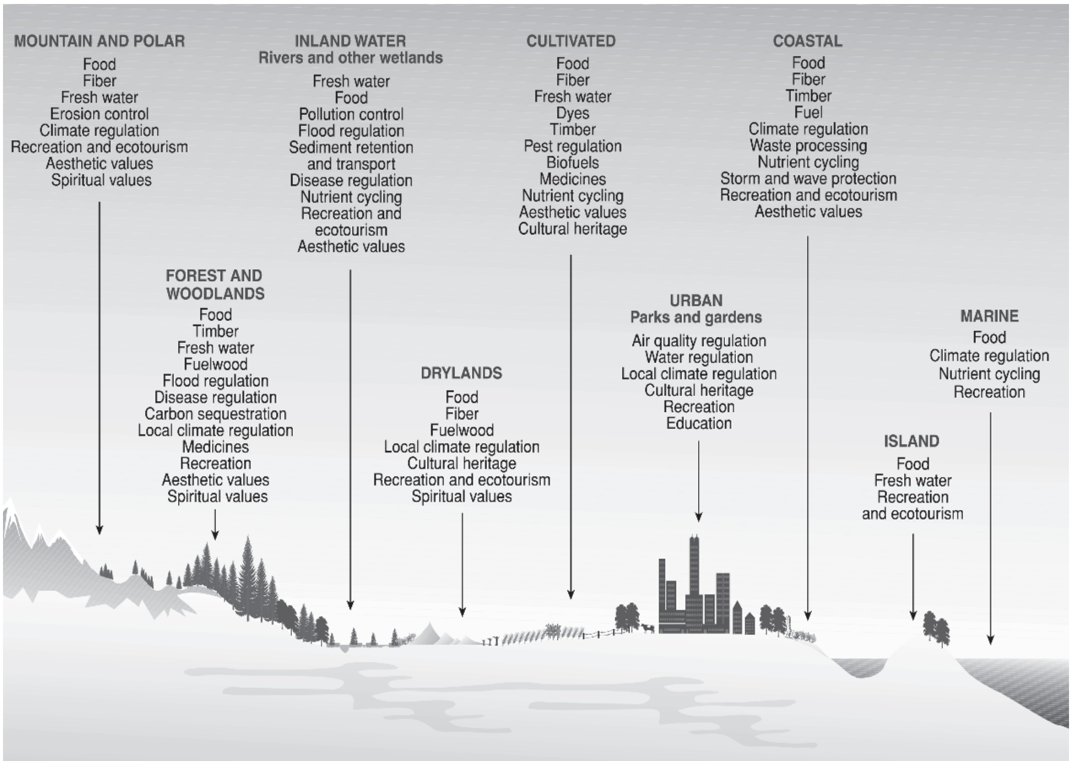

Figure 13.2. Kinds of services provided by various types of global ecosystems. The ability of ecosystems to deliver such services depends on complex biological, chemical, and physical interactions, which are in turn affected by human activities. (Millennium Ecosystem Assessment 2005.)

TABLE 13.2. Global status of world ecosystems as evaluated by the Millenium Ecosystem Assessement. Upward arrows indicate that, during the past 50 years, the ecosystem has been enhanced while downward arrows indicate degradation. ± indicate region-specific variability.

Service	Sub-category	Status	Notes
Provisioning Services			
Food	Crops	+	Substantial production increase
	Livestock	+	Substantial production increase
	Capture fisheries	–	declining production due to overharvest
	Aquaculture	+	Substantial production increase
	Wild foods	–	Declining production
Fiber	Timber	±	Forest loss in some regions, growth in others
	Cotton, hemp, silk	±	Declining production of some fibers, growth in others
	Wood fuel	–	Declining production
Genetic resources		–	Lost through extinction and crop genetic resource loss
Biochemicals, natural medicines, pharmaceuticals		–	Lost through extinction, overharvest
Fresh water		–	Unsustainable use for drinking, industry, and irrigation; amount of hydro energy unchanged, but dams increase ability to use that energy
Regulating Services			
Air quality regulation		–	Decline in ability of atmosphere to cleanse itself
Climate regulation	Global	+	Net source of carbon sequstration since mid-century
	Regional and local	–	Preponderance of negative impacts
Water regulation		±	Varies depending on ecosystem change and location
Erosion regulation		–	Increased soil degradation
Water purification and waste treatment		–	Declining water quality
Disease regulation		±	Varies depending on ecosystem change
Pest regulation		–	Natural control degraded through pesticide use
Pollination		–	Apparent global decline in abundance of pollinators
Natural hazard regulation		–	Loss of natural buffers (wetlands, mangroves)
Cultural Services			
Spiritual and religious values		–	Rapid decline in sacred groves and species
Aesthetic values		–	Decline in quantity and quality of natural lands
Recreation and ecotourism		±	More areas accessible but many degraded

Source: Millennium Ecosystem Assessment (2005).

for "sustained yield" much as we could "harvest" interest income from a bank account as long as we leave the principal intact. But a resource such as oil or coal, lying beneath the soil of a forest ecosystem, is also a stock-flow resource. In this case the transformation process, from biological material to a fossil fuel, has taken thousands or millions of years, but the resource can be – and is – extracted at an arbitrary and unsustainable rate or flow to be determined by human agents. As different as these two examples are from one another, they share common attributes of all stock-flow resources. First, stock-flow resources are those that have been materially transformed by ecosystem processes into usable goods. Second, they can be used at any rate desired, but, in many cases, some rates of use are too great to be sustained indefinitely. Third, stock-flow resources can be stockpiled or "stored up" for future use. They do not have to be used all at once, even if taken out of their ecosystem context. Finally, stock-flow resources can be used up, but not worn out.

In contrast, ecosystems also provide what can be described as ***fund-service resources***. A fund-service resource can suffer wear and tear from a production process, but it does not become a part of the thing it produces. Instead, the fund provides the service at a fixed rate, so the service is best measured in some metric that describes output over time. For example, terrestrial ecosystems are currently a net sink of CO_2 at a rate of 1.2 (±0.9) gigatons of carbon per year (MA 2005). By removing this carbon, such ecosystems provide a collective service to climate regulation and moderation. Such a service cannot be stockpiled (we cannot "store up" capacities for carbon removal this year to be used next year). The service must be delivered at a fixed rate. Thus, although the service cannot be "used up," it can be "worn out" if such ecosystems are degraded to the point that their ability to remove atmospheric carbon in greatly diminished.

13.1.3. Non-excludable and Non-rival Goods

As essential as such services are, they have proved repeatedly problematic for traditional economic theory at many levels. First, most of these services belong to an economic category known as ***non-excludable goods***. An excludable good or resource is one in which ownership of the resource permits the owner exclusive use of the resource, and provides the owner with the ability to exclude others from such use. But many ecosystem services are non-excludable. How would one, for example, exclude others from receiving the oxygen produced by the photosynthesis of trees in a forest? Even if one owned the forest, the breathable air it produces flows all over the planet, and all receive its benefits. Although some ecosystem services are or can be made excludable, many are and probably always will be non-excludable. Economists Herman Daly and Joshua Farley summarize the excludability problem eloquently: "If a good or service is not owned exclusively by someone, it will not be efficiently allocated or produced by market forces. The reason for this is obvious. Market production and allocation are solely dedicated to profits. If a good is not excludable, someone can use it whether or not any producer of the good allows it. If people can use a good regardless of whether or not they have to pay for it, they are considerably less likely to pay for it. If people are unwilling to pay for a good, there will be no profit in its production, and in a market economy no one will invest in producing it, or at least not to the extent that the marginal benefit to society of producing another unit is equal to the marginal cost of production (Daly and Farley 2004:157–158)."

A second problem of ecosystem services for traditional economics is that many of the goods and services produced are ***non-rival***. A ***rival good*** or service is one such that my enjoyment or use of the good or service infringes on your ability to enjoy the same good or service. If a pizza is set before us, every piece that I eat is a piece that you cannot eat, and vice versa. Thus the pizza is a rival good. But non-rival goods and services are those in which one person's use or enjoyment of the good does not affect or infringe upon the ability of others to use or enjoy the good. If an upstream wetland absorbs most of the water from a sudden downpour, and thus protects my downstream riverfront home from being flooded, it also protects my next-door, streamside neighbor just as much. My benefit of protection from the wetland does not in any way infringe on my neighbor's benefit of protection. We are both high and dry.

Because of their dependence on market mechanisms to allocate and set prices for resources, traditional economic theory has proven adept at the valuation and distribution of rival, excludable goods and services. But markets often fail to appropriately price, or sometimes even recognize, the sorts of goods and services that ecosystems provide. How can this problem be solved? Market-based approaches ask, can adjustments in market mechanisms themselves be used to solve this problem, and, in solving it, provide a basis for valuation of ecosystem services and the biodiversity they support?

13.2. Market-Based Solutions to Conservation Conflicts

13.2.1. The Role of Property Rights in Conservation

Some economists would argue that all conflicts between economics and conservation reflect a failure to clearly define and properly allocate property rights. If property rights are clearly defined and enforced, formerly non-rival, non-excludable goods and services, including those provided by ecosytems and biodiversity, can be made rival and excludable, and then subject to market mechanisms for valuation and allocation.

Drawing directly on Hardin's Tragedy of the Commons motif, economist Bruce Yandle describes a non-tragic ending to Hardin's story of the herders (whom Yandle calls "shepherds," making their livestock "sheep") and their common pasture. Rather than simply let the pasture go to wreck through unregulated grazing, the shepherds form a "shepherd's club" in which they share information and act cooperatively. Yandle states that "they may learn that each additional sheep reduces the weight gained for the collective flock. This marginal product, which is the change in total weight gained by the flock with the addition of one more sheep, declines faster than the average weight gained per sheep" (Yandle 1997:14). Yandle notes the shepherds will learn that "flock production would improve if fewer sheep were placed on the pasture. Pastures are depletable resources, but they are also sustainable. With appropriate safeguards, a shepherd community can engage in pasture rotation and maintain an economically efficient level of sustained use" (Yandle 1997:15).

Like all good economists, Yandle supports his thesis with a chart (Figure 13.3). Sheep enter the pasture as long as average weight gain is at least as good as the next best opportunity (any alternative pasture). Herd expansion stops when the marginal gain is negative. Using this relationship, Yandle notes that "the club would allow sheep in the pasture until opportunity cost was equal to the marginal product of the pasture, read at OA on the horizontal axis of the figure. Operating at that point, the shepherd club would produce the largest amount of weight gain possible: each member could conceivably be wealthier than before, depending on the rule for output sharing" (Yandle 1997:15).

The shepherd's club provides needed safeguards against overuse of the common-access pasture through shared information. However, the shepard's club does not solve the fundamental problem of property rights that pertain to the use of the pasture, a key element in effective resource and conservation management. To be most effective, property rights must be *transferable* or *tradable*. To understand how such tradable rights could serve conservation ends,

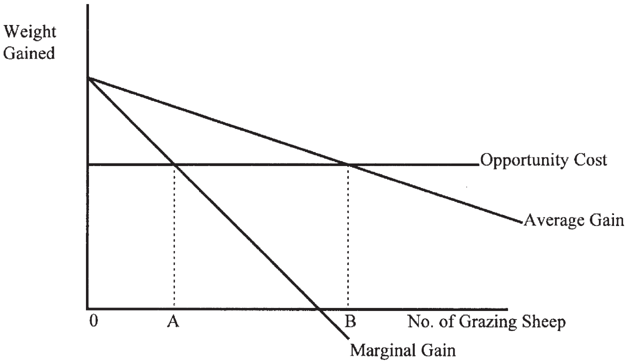

FIGURE 13.3. Hardin's (1968) tragedy of the commons expressed as a problem in marginal gains. The number of sheep entering the pasture (*x* axis) should be increased as long as average weight gain (*y* axis) is at least as good as the next best opportunity (any alternative pasture, represented by the line labeled "opportunity cost"). Herd expansion stops when the marginal gain becomes negative. Logically, a community of shepherds would allow sheep in the pasture until opportunity cost was equal to the marginal product of the pasture, read at OA on the horizontal axis. Operating at that point, the shepherds would produce the largest amount of weight gain possible. (Yandle 1997. Copyright 1997 by Rowman and Littlefield. Courtesy of Rowman and Littlefield.)

consider an historical example. In 1987, the combination of a mild winter with little snowfall, lower than normal spring rains, and a heavy demand for water for crop irrigation reduced the Ruby River in Montana (USA), normally a deep, swift flowing stream, to a mere trickle in many of its upstream reaches. Under these conditions, hundreds of trout became stranded in isolated and overheated pools where they could not survive. However, the diverted water turned out to be of low value to private landowners who had used it for crop irrigation and, because they diverted too much, ended up with excess water standing in their fields. A US conservation NGO, Trout Unlimited, wanted to temporarily purchase ("lease") water rights from the farmers and divert it back into the river to save the trout. Trout Unlimited had the money to do so, as the amount of water needed would have cost only US$4,000. Unfortunately, state and federal law prohibited transfer of water rights for "nonbeneficial" uses, traditionally interpreted to mean any use that did not benefit humans, such as irrigation, drinking, or human sanitation. Because saving the trout was not recognized as a "beneficial use" and the water rights were not freely tradable, water remained standing in crop fields while thousands of trout died (Anderson and Leal 1991).

Some economists believe that making property rights tradable, especially rights associated with ecosystem services, could avert conservation tragedies like Ruby River from recurring. But averting such tragedies is not merely a matter of making property rights tradable. It is also a matter of ensuring that property rights are "owned" at the most appropriate level for management. To understand the importance of appropriate level of ownership in conservation, we move from the Ruby River in the United States to the Communal Area Management Program for Indigenous Resources in Zimbabwe.

FIGURE 13.4. Populations of African elephants (*Loxodonta africana*), a species of conservation value, pose threats to crops, homes, and lives in native African villages in rural Zimbabwe. The Communal Area Management Program for Indigenous Resources (CAMPFIRE) establishes local citizen management cooperatives with well-defined property rights over wildlife resources, such that revenue derived from wildlife, in this case, elephants, is allocated to local communities that bear the cost of living with wildlife. (Photo by Will Simonson. Courtesy of A Rocha International.)

13.2.2. Biodiversity Conservation Through Market Incentive and Local Control

Conflicts between conservation efforts to preserve many African wildlife species, such as elephants (Figure 13.4), and local landowners, whose crops, homes, and, sometimes, lives are threatened by such wildlife lead to the development of the Communal Area Management Program for Indigenous Resources (CAMPFIRE) program in Zimbabwe, a radical departure from traditional command-and-control government-run programs to conserve African wildlife. In CAMPFIRE, management authority is delegated to district administrators of communal lands. Working with these district administrators, CAMPFIRE assists in establishing citizen cooperatives that have territorial rights (i.e. well-defined property rights) over wildlife resources. The majority of revenue generated from wildlife must be returned to the communities that bear the costs of living with the wildlife. CAMPFIRE has effectively generated revenue for local communities, primarily from safari hunting and ecotourism (Kreuter and Simmons 1995).

A similar approach, albeit in a very different setting, is found in the world's largest commercial cod fishery, the Lofoten fishery of Norway. Remarkably, there have never been any quota regulations in this fishery, nor any licensing system (Leal 1998). Rather, the government has, since 1897, given management authority to 15 "control districts," each of which has a well-defined territory and broad powers to develop and enforce district-specific fishing regulations (again, well-defined property rights). Enforcement is carried out by inspectors elected from within the fishing community for each type of fishing gear. Judgments against violators are rendered by local magistrates. All fishers must register with and obey the rules of the district in which they fish.

The Lofoten fishery succeeds because the fishermen can limit access to the resource, thus preventing over-exploitation. Similarly, oyster fishers in the US state of Louisiana, which permits private leasing of oyster beds, have earned more income from oysters on similar sized beds than their counterparts in adjacent Mississippi which has treated oyster beds as open access, public property resources. Louisiana oystermen also take a lower proportion of oysters early in the season, permitting better returns year round and greater long term conservation of oysters (Anderson and Leal 1991:124).

These examples are intriguing, but insufficient. We must ask, specifically, what relational mechanisms between private markets, scientific assessment of biodiversity resources, and government regulation are needed to make conservation work effectively in cooperation with market incentives? To gain this understanding, we now examine one case history in detail which reveals one model of interaction between market forces and government conservation regulations to protect a species of special concern.

13.2.3. Government-Market Coordination – Conservation and Paddlefish Caviar

In eastern Montana, the town of Glendive is home to approximately 8,000 residents. Its traditional economic base was agriculture, particularly cattle ranching. Located along the lower reaches of the Yellowstone River, Glendive is also famous for its paddlefish (*Polyodon spathula*, Figure 13.5), which spawn over gravel bars in swifter sections of this part of the Yellowstone. Paddlefish are highly valued as food, and even one individual can provide a lot of it. Typical adult paddlefish may be 5–7 feet long (including their paddle-like snout) and weigh 60–120 pounds. Each year, the paddlefish season (15 May–30 June) attracts about 3,000 anglers to Glendive. Because paddlefish feed mostly on plankton and other microscopic organisms, they cannot be caught with conventional bait and lures, but must be snagged. Fishers use large treble hooks on weighted, heavy lines, heaved into the river with surf rods 8–12 feet long.

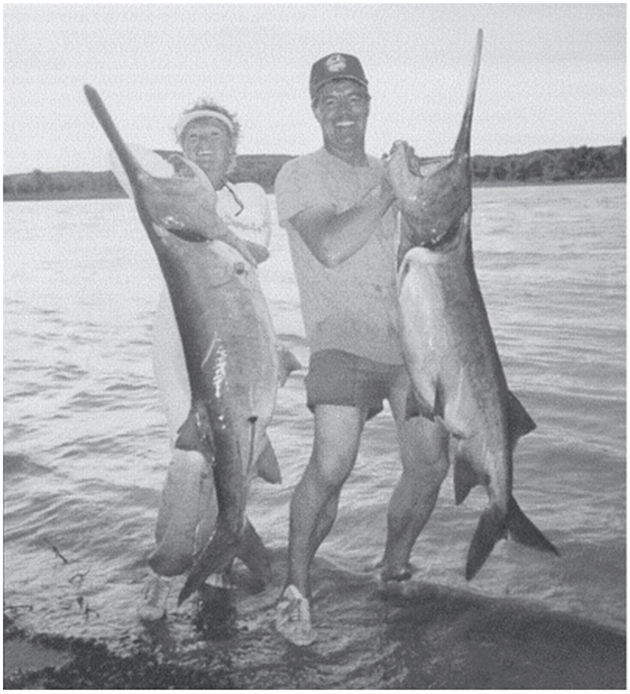

FIGURE 13.5. Paddlefish (*Polyodon spathula*) roe provides the basis for a growing caviar industry in Glendive, Montana. (Photo courtesy of Glendive Chamber of Commerce, Glendive, Montana, USA.)

Paddlefish roe (eggs) are used as caviar, comparable in quality to the more famous caviar of sturgeons (Family Acipenseridae). In the southern US, paddlefish populations in the Mississippi River and its larger tributaries have been over-exploited, resulting in the closure of many state fisheries in this region (Anderson and Leal 1997). Local entrepreneurs in Glendive, however, recognized that the fishers harvesting paddlefish from the Yellowstone and the nearby Fort Peck Reservoir and Lake Sakakawea, had no interest in the roe. In fact, fishers had historically dumped several tons of roe on the banks of the Yellowstone near Glendive each spring, attracting large concentrations of flies and rats, creating a public nuisance and health hazard. Glendive business planners conceived a plan to open a caviar processing plant and market the caviar internationally. Although the US Fish and Wildlife Service was reluctant to approve a project that might increase demand for paddlefish products, approval in the Yellowstone River rested with state officials of the Montana Department of Fish, Wildlife, and Parks. Biologists in the department determined that local populations of paddlefish appeared stable and secure. The paddlefish habitat in the river, reservoir, and lake also was reasonably well protected and not faced with any serious threats of pollution. The caviar plan did not increase mortality to the population or decrease recruitment, since the roe would come only from fish harvested by private anglers. However, to ensure the profit motives did not lead to overharvest, state officials stipulated that fishers had to donate their roe, not receive payment for it. To make this attractive, the Glendive community agreed to employ individuals who would clean an angler's paddlefish without charge. In return for the cleaning service, the cleaner would keep the roe and give it to the caviar factory. Finally, the state stipulated that, in addition to a regular fishing licenses, paddlefish anglers would be required to purchase special paddlefish tags that must be affixed to each fish caught (Anderson and Leal 1997). In order not to favor the affluent, the cost of the paddlefish tag was low (in 2007, US$6.50 for Montana residents and US$15 for fishers from out of state), but the number of tags that can be sold was fixed. In this way, state officials were able to control the maximum number of paddlefish that could be harvested in a season, while making a food resource and recreational opportunity accessible to all citizens. Finally, the Glendive business community agreed to devote half of the net revenues from paddlefish caviar to the state of Montana for paddlefish research and management (Anderson and Leal 1997). In its first 7 years of operation, the project grossed over $1 million in revenue.

In our examination of values and ethics in conservation (Chapter 2), we noted the dangers of tying conservation to market-driven demand, particularly in the example of the green turtle. We would be wise to remember now the words of conservation biologist David Ehrenfeld regarding this example. "The power of global demand erodes all safeguards.… the commercial ranching of green turtles inevitably brings us around again on the downward spiral – a little closer to the extinction of the remaining populations. By no stretch of the imagination is this conservation" (Ehrenfeld 1992). But there are differences between paddlefish caviar and sea turtle ranching. These differences can be isolated in six elements of the paddlefish example that have general applicability to a successful interaction between governmental authority and free market systems.

Element One: The resource to be used was derived from stable populations whose habitats are protected and managed for the population's benefit – The state, not the market, made biological determinations of the status of the population and its habitat. The sustainability of both were mandated as given conditions required *a priori* by state regulatory authority as pre-requisites for any use of the paddlefish as a human resource.

Element Two: The persistence of the resource in perpetuity is mandated, regardless of market comparisons of present versus future values or considerations of opportunity costs – The market was not consulted about whether paddlefish habitat could be used more profitably for other purposes, or whether the current value of paddlefish at higher rates of exploitation had more value than the future or option values of paddlefish populations in future generations. The persistence of paddlefish in Montana was non-negotiable, set above the reach of the market by the state's statutory authority, implicit in both its laws and in regulatory policies that enforced them.

Element Three: The rate of exploitation of the resource was determined by biological criteria, not economic criteria – Optimal exploitation rates of paddlefish were not determined according to the criteria of profit maximization, supply and demand, or human welfare. The exploitation rate was determined by the biological productivity of the local paddlefish population as determined by biologists, and exploitation was set at a rate below maximum sustainable yield in order to ensure continuance of a stable harvest.

Element Four: The harvest was administered by the state in a manner that ensured that maximum sustainable yield was not exceeded, and in a way that removed profit incentives to violate yield restrictions – By requiring every paddlefish to be tagged and having game wardens arrest violators, the state enforced the conditions described above without regard to market values. By making the tags inexpensive despite their scarcity, the state made opportunity to harvest the resource independent of market forces that would have favored the affluent. By requiring roe to be donated rather than sold, the state removed profit incentives to harvest more paddlefish than had been allowed by law.

Element Five: Regulated private enterprise was allowed to create a market for a natural resource, to allocate the distribution of the resource according to supply and demand, and to permit the private sector to receive an economic incentive – With restrictions that prevented the market from determining the *amount* of the resource that could be harvested, the market was permitted to determine the *value* of the resource that was harvested. A portion of the profits went to those who marketed the resource, giving them incentive to continue, and placing an economic value on the resource itself.

Element Six: Profits were tied to resource sustainability by mandating that a portion of the profits be reinvested in the productivity of the resource, not in expanding the production or harvest capacities of the market – Historically, profits from commodity resources have been used to increase the capacity of exploiters to take more resources at faster rates. This pattern increased short-term profits, but destroyed long-term sustainability. In Glendive, profits were directed to improve the productivity of the resource, thus enhancing its sustainability. More profits can come from larger harvests, but only if the investments lead to larger populations that produce larger yields. Here a system was established which couples economic profit with biological productivity.

Not all forms of resource use lead to resource depletion, and not all forms of resource use lead to habitat degradation. When this is the case, conservationists can work with the private sector to create markets for resources that assign specific economic values to benefits derived from such resources. The lesson from Glendive is straightforward when coupled with lessons from conservation history. The market is a bad master for conservation values, but it can be made a useful servant to achieve conservation ends, if its mechanisms are channeled to achieve profit according to predetermined, community-based conservation values enforced by government regulation at levels determined by scientific assessment. Administered wisely, the coupling of conservation values and market incentives can produce and efficiently distribute benefits that build broad-based, community-level support for conservation more efficiently and effectively that legislative mandate alone. Such efforts move the concept of sustainability beyond the academic and professional culture of conservation biology into the world of private business and economics. In this case, the citizens of Glendive came to understand that a healthy, stable population of paddlefish was an index of their community's well being. Decline in the population would be viewed by them as a symptom of distress.

POINTS OF ENGAGEMENT – QUESTION 1

What conservation efforts could be more effective if the conservation goal for a given population was coupled, under appropriate regulation, to a market-driven incentive, and how could such a coupling be created without threatening the population?

13.2.4. Integration of Conservation Assets in Private Property Value

13.2.4.1. Zoning Laws and Conservation Easements

Property rights are not necessarily individual. They can be held by communities (as in Yandle's "shepherd's club"), the government, or no one. Advocates of property rights solutions to biodiversity conservation often assume that the best results come from greater levels of private ownership and higher allocations of property rights to private individuals, but these are not the only property rights-based solutions available.

Zoning is an arrangement in which some of the property rights normally associated with the individual owner of a property are transferred to or held by the community in which the property is located, effectively restricting what individual property owners can do on their property because of the context in which the property is located. For example, if my home in my town is in a section that has been zoned "Residential," I am not at liberty to tear down my home and build a five-star hotel or a glass factory, even if I have sufficient land and money to do so. The community, more specifically the city council, has determined that those sorts of enterprises must be placed in zones designated as "commercial" or "industrial." In effect, zoning is a form of land use regulation which asserts that the public can limit future development to protect public interests, and that compensation is not necessarily provided. I could petition the City Counsel for an exception to the zoning restriction if I can show that such an exemption would be warranted. But my petition will be made public and debated in an open hearing that any of my fellow residents might attend. The decision will be made by community deliberation, not market forces or prices. If my request is denied, I have no basis for asking the city or my neighbors for potential lost income that I could have received from making windows in my factory or from guests using my hotel.

Zoning represents the "police power" of the public to regulate "external" costs associated with individual decisions of private landowners. The zoning ordinance in my example is a pre-emptive strike by the community that prevents me or anyone else from placing undue levels of noise, traffic congestion, or potential environmental hazards in the proximity of where people live. Thus, zoning can be a critical tool for private land conservation. If my community zones an area around the town as "open space" or "native prairie," they are specifying a land use that no private landowner can violate. Thus, zoning regulations can act as an incentive for conservation by limiting the size and intensity of development, or even banning it altogether.

Zoning has implications for conservation because zoning regulations can reduce the cost of purchasing development rights. That is, if a potential land buyer is a conservation NGO such as The Nature Conservancy, and if they know that the land they want is situated in a location that has already been zoned "open space," they know in advance that the owner has no basis to raise her price to what the land would be worth if converted to an industrial park or a new housing development, and no hope of getting such a price from any buyer. Thus, zoning designed for conservation can lower the "ceiling" of expected costs for land acquisition and use, and give individuals or organizations intending to use the land for conservation purposes a significant advantage as buyers. Conservation programs can take advantage of the restrictions that zoning imposes because the developable land value is lower than it would be without regulation.

Conservation easements are a special case of land use zoning, applied specifically to conservation, and were developed to make the value of conservation on private land more explicit and more profitable to landowners. In an easement, the landowner agrees, usually with a government entity or a private conservation organization, to restrict some activities or forms of development on his or her land to achieve specific conservation goals, such as habitat or species protection. Such restrictions lower the assessed value of the land, generating a reduction in property taxes for the owner and a reduction in inheritance taxes for the owner's heirs. The owner, however, retains possession, residence and non-prohibited activities, and legal title to the land. Conservation easements work because they provide incentives for conservation by private citizens on their own land, and permit management objectives that focus on the biological and community-based integrity rather than on individual species.

13.2.4.2. Hedonic Valuation Models for Private Property

One of the long-term goals of conservation in socio-economic context is to move local residents from a reactive posture that denies responsibility for the current state of a site to a proactive posture that not only accepts, but anticipates, responsibility for the site and does even more than is required in its restoration (Clarkson 1995; Table 13.3). One way to illustrate these principles is to see how environmental quality can be treated as a "value added" dimension of private property exchange in a developed setting. For that illustration, we look to an application of this method in the US state of California.

The California counties of Contra Costa, Santa Cruz and Solano surrounding the San Francisco Bay area include residential property valued among the highest in the United States. In these counties, resource economists Carol Streiner and John Loomis estimated the economic value of various measures of stream restoration to private property values using a ***hedonic property model*** that treats property value as a function of its structural characteristics (*S*), neighborhood (*N*), and environmental quality (*Q*), expressed in the identity

$$P_i = f(S_i, N_i, Q_i)$$

where the subscript *i* refers to each value for an individual (*i*th) property (Streiner and Loomis 1996). Because attributes of property value are typically grouped, Streiner and Loomis created "restoration packages" that could be applied to different properties (Table 13.4). Restoration package A included improving fish habitat and the acquisition of additional land along the stream by the California Department of Water Resources Urban Stream Restoration Program for a streamside education trail. Restoration package B featured properties where streams were restored in ways that reduced flood damage, cleaned up, revegetated and stabilized the stream bank, cleared obstructions from the stream channel, and added aesthetic elements such as check walls, rock or stone walls or wood plank walls along the stream.

Streiner and Loomis determined that individual elements of package A added $15,000–$19,000 in property value. In package B, only stabilization and reduced flood damage added value, but these increased worth by up to $7,800. A joint model incorporating dimensions of both packages added over $19,000 in value to in average value to individual properties (Table 13.4; Streiner and Loomis 1996). This analysis demonstrated that not every type of restoration added significantly to private property value, but many did. Restorations that added value included both efforts that restored inherent functions of the stream (e.g., improved fish habitat) as well as those that more directly benefited the property owner (e.g., reduced flood damage).

TABLE 13.3. Categories of participant attitudes and strategies in conservation and environmental restoration efforts.

Participant Attitude	Participant Strategy	Participant Performance
Reactive	Denies responsibility	Does less than required
Defensive	Admits responsibility but resists it	Does the least that is required
Accomodative	Accepts responsibility	Does all that is required
Proactive	Anticipates responsibility	Does more than is required

Source: From concepts from Clarkson (1995). Table format by M. J. Bigelow.

TABLE 13.4. Values of alternative "conservation packages" associated with stream restoration efforts adjoining private residential property in Contra Costa, Santa Cruz, and Solano Counties, California.

Restoration Measure	Absolute Value of Restoration	Value of Restoration Relative to Property Value (%)
Restoration Package A		
Fish habitat improvement	$15,571	11
Land acquisition for education trail	$19,123	13
Education trail established	$17,560	12
Restoration Package B		
Streambank stabilization	$4,488	3
Reduced flood damage	$7,804	5
Joint Model		
Education trail established with streambank stabilization	$19,078	13

Source: Adapted from Streiner and Loomis (1996). Table format by M. J. Bigelow.

POINTS OF ENGAGEMENT – QUESTION 2

The previous example describes a situation where stream restoration was necessary because of degradation caused by private residential development. Imagine yourself as a private developer of residential property that included riparian habitat. What development strategy would you employ to conserve the values described above so that they added value to the initial sale of the property rather being lost in the construction process?

13.2.5. Can Property Rights Enhance Conservation in Wildlife Refuges? The Case Histories of Rainey and Baker Wildlife Sanctuaries

The Audubon Society, a private conservation NGO, has an admirable record of biodiversity conservation. As part of its conservation effort, the Society purchases and manages lands of high conservation value as wildlife sanctuaries. One of these is the Rainey Wildlife Sanctuary in Louisiana (USA). Rainey is home to mammal species such as white-tailed deer, armadillo, muskrat, otter (*Lontra canadensis*), and mink (*Mustela vison*), as well as hundreds of species of birds. As an organization, Audubon opposes drilling for oil and natural gas in wilderness areas in the US. But it takes a different view when its own property rights, in this case on the Rainey Wildlife Sanctuary, include the rights to these resources. Since the 1960s Audubon has permitted the development of oil wells within Rainey, even though these are a potential source of pollution and other threats to wildlife. Yet, carefully monitored and constrained, Audubon has found, over the past 4 decades, that oil can be extracted without measurable damage to the marsh. From the beginning, the Society put extra precautions in place to prevent pollution, and these have proven effective for over 40 years. In return for allowing an oil and gas production company, Consolidated Oil and Gas, to remove oil and natural gas on the sanctuary, Audubon receives royalties. However, because the Society is concerned first and foremost with the conservation of biodiversity, they imposed contractual restrictions on the company regarding how the oil could be extracted. These restrictions increase the company's extraction costs, and this additional cost reduces the royalty that Audubon receives compared to what it could get without regulations. That, as economists Terry Anderson and Donald Leal note "is the price they pay for caring for the environment" (Anderson and Leal 1991:91).

Given the precedent set by oil development at Rainey, the Society considered a similar proposal to drill for oil at its Baker Sanctuary in Michigan (USA). However, the Society's own bylaws prevented such development on that refuge, and an initial proposal to Audubon members to make an exception in this case was voted down. Eventually the membership did pass an amendment to the bylaws to allow directional drilling off the refuge to remove oil from beneath the refuge, an effort that began in the spring of 1981. Anderson and Leal note that Audubon placed rigorous restrictions on the drilling at Baker Sanctuary to protect that refuge's wildlife, but permitted the drilling to raise more money to conserve biodiversity at national and international levels. "Given an operating deficit of $14,000 and the technical capabilities of directional drilling, the Michigan Audubon Society decided to allow Michigan Petroleum Exploration to explore the marsh. Michigan Petroleum was required to use directional drilling from a pad a half-mile from the marsh, use high efficiency mufflers to minimize noise, contain drilling fluids, and finance studies of possible environmental problems. The Society received royalties of approximately $1 million, probably less than they could have obtained had they not demanded strict environmental controls" (Anderson and Leal 1991:91). Even off site at the drilling pad, the Society was sensitive to possible disturbance that the drilling might cause resident birds. Journalist John Mitchell, writing in the Society's *Audubon* magazine, chronicled his firsthand experience of the operation. Describing events from the offsite drilling pad, he wrote "They had just broken ground for the drilling pad, last time I went out to Big Marsh Lake.… Three or four weeks probably, and a sky full of sandhill cranes would be splashing down out there in the marsh. That's why the hardhats were in a hurry. They had to get the pad in, and find what they were looking for beneath the marsh, and get out themselves for a while, before the cranes returned. That's the way it was written in the contract. There was this timelock, and when the cranes punched in, the hardhats would have to punch out" (Mitchell 1981:16) (Figure 13.6).

Is Audubon's action an example of practical and productive conservation policy, or a disturbing case of compromise and rationalization counter to their own conservation ideals? This tension is not confined to Aududon. Commodities like oil and natural gas have established markets that determine their prices. Such commodities may generate revenues that can be reinvested in conservation, but the commodities are not what NGOs like Audubon are trying to conserve. Free-market environmental economists like Anderson and Leal advocate the competitive, private auction of lands with high values for wilderness or wildlife conservation to those who are willing to pay the most for them. By some measures, this would certainly represent what free-market economists would define as "efficient" allocation, but it is hard to imagine even the most well-financed conservation NGOs, like The Nature Conservancy, being able to "outbid" Exxon Mobil for a wilderness area or natural sanctuary that both desired. As environmental ethicist Mark Sagoff noted earlier (Chapter 2), such a strategy would

FIGURE 13.6. The Audubon Society's Baker Sanctuary in Michigan (USA). Here Audubon permitted directional drilling off refuge, under strict supervision, to remove oil beneath the refuge, reducing environmental risks and using royalties to fund portions of its conservation efforts. (Photo by Mike Boyce, used by permission. Copyright Mike Boyce.)

circumvent the role of public, community discussion and deliberation about what might be the "best" use of such lands. But Leal and Anderson respond by proposing the creation of "Conservation Endowment Boards." Under this arrangement, national conservation boards, with members approved by a country's national Congress, would each have a narrowly defined mission of protecting and enhancing a specific conservation value. In their own words, Leal and Anderson describe the arrangement as one where "Each board would have a fiduciary [fiduciary means "of or relating to holding something in trust for another"] responsibility under common law to carry out a single mission, and it would have the option of allowing alternative uses in the area as long as those uses enhance the board's overall mission." Radical as this idea may seem, the Rainey and Baker Sanctuary case histories are examples of this principle in action. In this case, the "endowment board" was the Audubon Society. It held in trust, for its members, a mission to protect biodiversity, but was willing to allow other activities on its refuges if they contributed to that mission. So perhaps such a proposal is not so radical as it might first appear.

If markets can generate value for resources on refuges, can the biodiversity of the refuge itself, described by some as an "amenity" rather than a commodity, also find a "market" that will determine its value and generate revenue for its continuance?

13.2.6. User Fees on Public and Private Lands – Pricing the Value of Conservation

We have already explored (Chapter 2) how various techniques of contingent valuation, such as Willingness to Pay (WTP) and Willingness to Accept Compensation (WTC) can be used to create "shadow markets" for nonmarket goods associated with ecosystem services by attempting to determine consumer and user preferences. And we have also seen that such methods suffer from both technical difficulties as well as moral and ethical objections over their tendency to confuse values with benefits (Sagoff 2000). But what if the valuations of such activities were not determined by a shadow market but by a real one? To create such a market so that "amenities" can be valued similarly to commodities, many economists advocate greater employment of "user fees."

User fees, as their name suggests, are monies paid for the privilege of using a specific area for a specific purpose. For example, campers using a campground in a national park or forest are accustomed to paying a daily or weekly fee for the privilege of using the campground, and, in a "developed" campground, for services provided like showers, drinking water, toilets, fire pits, picnic tables, firewood, and parking spaces. Similarly, anglers and hunters pay fees to obtain licenses for the privilege of fishing and hunting on both public and private lands. What if fees were also charged for trail use, wilderness camping, stream access (for fishing), picnicking, road use (to get to the trailhead) or bird watching? The idea of user fees for these sorts of activities is unpleasant to citizens of countries like the United States where such activities on public lands have a long history of being a "right" of every citizen, but such fees do have the effect of generating income from conservation-friendly activities, and increase motivation among managers to preserve the associated biodiversity. Randall O'Toole, a former economist with the US Forest Service, has gone so far as to assert that user fees are the single most important component needed to reform that agency from being controlled by commodity interests such as grazing, mining, and logging, to becoming an agency that truly preserves the national forest heritage. In his ground-breaking book, *Reforming the Forest Service*, O'Toole wrote, "Most forests could produce fees averaging $3 per visitor per day.… At this rate, recreation would be the main source of national forest income throughout the Rocky Mountain and Intermountain regions, Alaska, the New England and Midwestern forest, and the Southern mountain forests.… At $3 per visitor day, total income will exceed $900 million in 1990" (O'Toole 1988:191).

O'Toole published these words in 1988, but, with adjustment for inflation, it is not difficult to see that, in the twenty-first century, user fees on US National Forests could generate revenues in the billions of dollars. And the same is true in parks, forests, and refuges throughout the world. In fact, much of what O'Toole wrote in the 1980s and 1990s is not longer a controversial proposal but established policy, as agencies like the Forest Service have adopted user fees, whenever possible, and generated massive amounts of revenue from doing so. On public lands, where the state or federal government holds most of the property rights, user fees flow back into agency bureaucracy, hopefully to be spent to enhance the "amenity" the user desires. But user fees, often in the form of access fees, also have a history of success in the private sector as long as a private landowner has well defined and tradable property rights that she may offer to others in exchange for payment. For example, in England and Scotland, where public lands are fewer and smaller, a relative scarcity of fishing opportunities in freshwater streams has encouraged the development of attaching property rights to fishing sites. Such an arrangement has a long history in the United Kingdom, where angling traditionally has been considered an accessory right of riparian ownership. Thus, English landowners are permitted to lease their fishing rights to nonriparian landowners willing to pay their price. Given such an arrangement, coupled with increasing scarcity of high quality fishing streams in their country, few British landowners can ignore the commercial aspect of the fishing rights they own. As Anderson and Leal note, "it has become worthwhile for British landowners to incur the costs of specifying and enforcing contractual arrangements that govern fishing. As a result, many private, voluntary associations have been formed to purchase fishing access rights" (Anderson and Leal 1991:112). The British fishing expert Brian Clarke has noted this development and its effect on the quality of fishing in his country, because it gives landowners incentive to improve stream habitat to capture greater benefit from greater demand from anglers to use their stream instead of their neighbors. "In the 1960s and 1970s, smaller, privately managed fisheries that offered exclusivity in exchange for higher rod fees began to break out like an aquatic rash around the country [England]. Now every city and major town … has first-class trout fishing within easy reach, and at an affordable price" (Clarke 1979:219). In contrast, some economists and private landowners in countries like the US which have strong histories of open access to streams and rivers, claim that the lack of such transferable property rights acts as a perverse incentive to landowners to let their streams degrade, thereby reducing incentive for anglers to trespass their property and expose them to increased risks of liability.

How do we determine what fees to charge on public lands? One technique is to determine market price for services of this kind is through *travel cost estimation*.

13.2.7. The Travel Cost Method – Estimating the Value of a Costa Rican National Park

The ***Travel Cost Method*** (TCM) is an economic method of determining environmental values that belongs to a larger family of behavior-based, analytical economic techniques called ***revealed preference methods***. TCM works on a simple but reasonable assumption: the more valuable an environmental resource or amenity, the farther people are willing to travel to experience it, the more they are willing to spend per trip, and the more trips they are willing to make. Such variables can be integrated, at least in part, through a TCM demand curve such as that shown in Figure 13.7. Here the cost per trip (a reflection of distance, *y* axis) is related to the number of trips a person makes to the site that contains the amenity or resource (*x* axis). Note that as the cost of the trip rises, the number of trips decreases. TCM also can be effective if it is used in a "before" and "after" approach to a site, such as a comparison of visitation before and after an environmental improvement (e.g., creating a lake for fishing).

In traditional economics, the supply and demand curve relates price to quantity demanded; in a TCM curve, travel costs are the analog of price and number of trips the analog of demand. If a person is willing to make six trips, each costing \$20, then the person's willingness to pay is 6 × \$20 or \$120. This willingness to pay is also referred to as *consumer surplus*. Aggregate consumer surplus is calculated as the area under the TCM demand curve (Loomis 2000). If we want to compare two different areas, and we suspect

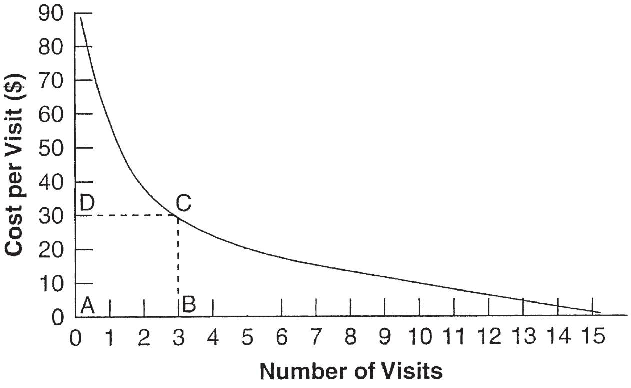

FIGURE 13.7. A travel cost method (TCM) demand curve that estimates the value of an environmental amenity, such as a national park. Unlike a neoclassical supply and demand curve, the TCM demand curve makes travel costs (*y* axis) serve as the analog of price, and number of trips (*x* axis) the analog of demand. Willingness to pay for the environmental amenity or service is represented by the area ABCD and its value is the product of travel costs and number of trips. In this example, if it costs \$20 for a trip to the park, five trips will be taken, so a value of \$100 represents the value of the park to the individual. (Drawing by M. J. Bigelow and F. Van Dyke.)

that one area is of higher environmental quality, we could calculate the TCM demand curves for both areas. If our hypothesis is correct, the TCM demand curve from the better environmental area should lie to the right of the other.

In addition to its usefulness in estimating values of consumer surplus, values of environmental improvements, and relative values of different areas, TCM also can be useful to managers in setting prices for entry fees. The Costa Rican National Park Service learned, through TCM analysis of three of its parks, that a common fee was not the most economically efficient method of raising revenue because tourist demand differed among parks (Figure 13.8; Chase et al. 1998). Not only did the demand curves show different *y* intercepts and slopes, but they also had different shapes. The Park Service could potentially use such data in four alternative ways, depending upon their objective:

Objective One: Maximize revenue generated from entrance fees and estimate total maximum revenue from the three parks. This objective can be achieved by determining the maximum product of *x* (number of visitor days) and *y* (entrance fee). For example, if the managers charge a $10 daily fee at Manuel Antonio Park, they can expect 4,000 visitor days, or a revenue of $40,000. If, on the other hand, they charge an entrance fee of $22.50, use days are cut in half (2,000 visitor days) but revenue increases to $45,000.

Objective Two: Minimize financial cost to the parks. Perhaps the National Park Service has a limited budget and insists that parks be self-supporting through the collection of daily fees. If we assume that costs increase with increasing numbers of visitors, then it should be possible to determine a "supply curve" that relates visitor days to park costs. Where park costs per day intersect the demand curve of the daily entrance fee, supply equals demand. If the entrance fee is set below this point, visitor days increase as costs increase, but revenue decreases, creating a deficit. If the fee is set at a higher level, revenues may exceed cost, but the park is "underused" in terms of services that could be provided. Of course, park costs may be a constant; that is, perhaps it costs just as much to manage the park whether any visitors come or not. If this is the case, then the "supply" curve is simply a horizontal line. But it is still valuable to determine the point at which it intersects the demand curve of the entrance fee-visitor day relationship because that point represents the *minimum* entrance fee that must be charged to recover costs of operation.

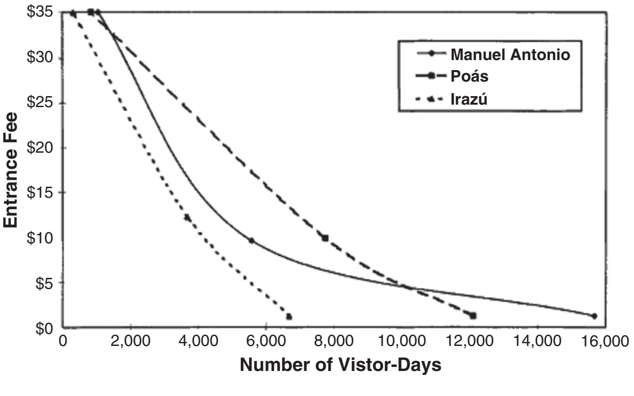

FIGURE 13.8. Demand curves associated with three Costa Rican national parks that relate entrance fees to visitor use days. Such demand curves, properly estimated, can be used to answer questions about various economic and ecological strategies for the parks. (After Chase et al. 1998.)

Objective Three: Minimize environmental cost to the parks. As noted in the story of the Bonaire Marine Reserve (Chapter 11), increased visitation almost certainly will increase environmental degradation to a park. If the Park Service can determine a maximum acceptable threshold of such damage, beyond which further damage would degrade or destroy the park's value and purpose, they can theoretically determine the threshold number of visitor days allowable, and set revenues to create this level of demand. Using this strategy, price is actually used as a tool to control or limit demand, and through such control to limit degradation to the environment. By limiting degradation, park managers may enhance persistence and diversity of populations that can continue to reside within park boundaries, and decrease operational costs of park management and maintenance.

Objective Four: Set an entrance fee that is appropriate to the actual incomes of most native Costa Ricans to ensure that nationals are not "priced out" of their own parks by wealthier foreign tourists. Here the demand curve can be used to address an issue of access and social equity. An entrance fee of $17 per day may increase revenues compared with one of $5, and European or North American tourists may be willing to pay it. Average-income Costa Ricans however, may not be able to visit their own park! If the Park Service considers that such a condition represents an injustice to its own citizens, it would choose a fee appropriate to average national income. Using its demand curve, it would then be able to predict expected visitor days and make its management plans accordingly. In fact, many countries do take such income discrepancies into account, and charge a lower entrance fee for their own citizens than for foreign visitors.

Optimizing outcomes for these four objectives illustrates the usefulness of the demand curve to achieve an economically efficient solution. This example also illustrates the inadequacy of economic data, by themselves, to achieve anything "good" unless we first determine which "good" we want to achieve. Thus, moral choice – the deliberate and predetermined objective to reach the highest and best outcome – is an essential element in our use of an economic analysis and should be intentionally considered and scrutinized when we consider the relationship of economic activity and conservation. Free market economists see answers to these kinds of conservation dilemmas in better definitions of property rights and coupling to market mechanisms. But others, the "ecological economists," believe that an entirely different approach is necessary.

13.3. Ecological Economics

13.3.1. General Considerations

In his landmark book, *The Environmentalism of the Poor*, economist and economic historian Joan Martinez-Alier of the University of Barcelona (Spain) takes a position regarding economics and the environment very different from free-market economists like Anderson and Leal. He writes, "In modern industrialized and industrializing societies there has been a strongly argued view that enlarging the economic pie (GNP growth) represents the best way of alleviating economic distribution conflicts between social groups. The environment came in, if at all, as an afterthought, as a preoccupation arising out of deeply held values on the sacredness of Nature, or as a luxury (environmental 'amenities' rather than necessities). The poor were 'too poor to be green'. They must 'develop' to get out of poverty and, as a by-product, they could then acquire the taste and the means to improve the environment" (Martinez-Alier 2002:16). Martinez-Alier offers a different view. He argues that conservation is not to be treated as an amenity, but as a necessity, especially for the poor. And the affluent of wealthy nations will not enhance environmental conservation and biodiversity protection by increasing their technological efficiency in waste disposal and fuel consumption, but by increasing their frugality through limiting how much they use and consume.

Thilo Bode, former executive director of Greenpeace, wrote to the journal *The Economist* after World Trade Organization (WTO) meetings in Seattle 1999, which were marked by violence and rioting directed against the WTO, "You claim that greater prosperity is the best way to improve the environment. On what economy's performance in what millennium do you base this conclusion?… To claim that a massive increase in global production and consumption will be good for the environment is preposterous. The audacity to make such a claim with a straight face accounts for much of the heated opposition to the World Trade Organization" (quoted in Martinez-Alier 2002:16).

In his *Essay on Population*, the economist Thomas Malthus (Figure 13.9) wrote, "Population, when unchecked, increases in a geometric ratio. Subsistence increases only in an arithmetic ratio. A slight acquaintance with numbers will shew the immensity of the first power in comparison with the second.… In two centuries and a quarter, the population would be to the means of subsistence as 512 to 10." Malthus predicted that populations would grow beyond their means of subsistence, and only "misery and vice" would keep numbers in check (Piel 1995).

FIGURE 13.9. Thomas Malthus, an English cleric and economist, whose *Essay on Populations* proposed that human populations are limited by environmental constraints and resource scarcity.

Despite his mathematical logic, Malthus' conclusions were generally disregarded because they appeared to be refuted by actual human experience. Human ingenuity and technology have, in fact, shown far more than arithmetic increase. World human population is now in its third doubling since Malthus published his *Essay*, and has been sustained by more than five doublings of "the means of subsistence" (world per capita GNP). Even since 1950, industrial technology (overriding any arithmetic constraint) has twice doubled the output of material goods (Piel 1995). With this record of achievement and growth in both population and affluence, neoclassical economists could safely ignore Malthus' ideas and treat his essay simply as an historical footnote.

Not all economists, however, were prepared to dismiss Malthus' views on growth and its limits. One of the most influential modern economists to address the problem of environmental constraints was Nicolas Georgescu-Roegen. In his classic work, *The Entropy Law and the Economic Problem*, Georgescu-Roegen argued that, "What goes into the economic process represents *valuable natural resources* and what is thrown out of it is *valueless waste*" (Georgescu-Roegen 1993:76, emphasis his). "… Matter-energy," Georgescu-Roegen continued, "enters the economic process in a state of *low entropy* and comes out if it in a state of *high entropy*." Entropy is a measure of the amount of unusable energy in a system;

as entropy increases, the amount of energy available for work decreases. To illustrate, Georgescu-Roegen asserted, "… a piece of coal can only be used once. And, in fact, the entropy law is the reason why an engine (even a biological organism) ultimately wears out and must be replaced by a *new* one, which means an additional tapping of environmental low entropy" (Georgescu-Roegen 1993:80).

To better illustrate the relationship between economic processes and entropy, Georgescu-Roegen compared the Earth's resources to an hourglass full of sand (Figure 13.10), in which the sand in the upper part of the hourglass represented the store of low-entropy resources. Its rate of movement into the bottom of the hourglass was its "flow," controlled by rates of solar inputs. As the amount of low-entropy resources diminished, the amount of high entropy waste (in the bottom of the hourglass) increased and accumulated. Some of the upper sand coalesced into clumps and might move through the neck of the hourglass all at once, analogous to fossil fuels that might accumulate large quantities of solar energy and then can be tapped at higher rates of flow. But regardless of the rate of flow, the sand in the upper half is destined to run out. And, unlike a real hourglass, this one cannot be turned over! Although humans have almost complete command of the energy stocks, for all practical purposes, they have no control over the flow of solar radiation. To Georgescu-Roegen, the implications of this understanding were profound: "There is an important asymmetry," he noted, "between our two sources of low entropy. The solar source is stock abundant, but flow limited. The terrestrial source is stock limited, but flow abundant (temporarily). Peasant societies lived off the solar flow; industrial societies have come to depend on enormous supplements from the unsustainable terrestrial stocks." The principal question was not, therefore, "How many people can the Earth support?" but "How long can a population of any given size be maintained?" Thus, Georgescu-Roegen wrote, "Every time we produce a Cadillac, we irrevocably destroy an amount of low entropy that could be used for producing a plow or a spade. In other words, every time we produce a Cadillac, we do it at the cost of decreasing the number of human lives in the future" (Georgescu-Roegen 1993).

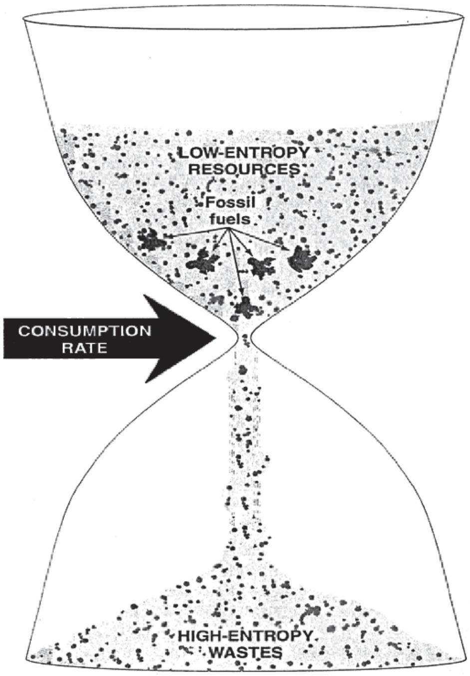

Figure 13.10. The "hourglass analogy" of economist Nicolas Georgescu-Roegen illustrates the relationship between entropy and economics. The sand in the upper part of the hourglass represents Earth's low-entropy resources. As humans consume these resources, high-entropy wastes are produced. Regardless of the consumption rate, the sand in the upper half is destined to run out. (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications,* Copyright 2003, McGraw-Hill Publishers. Reprinted with permission of The McGraw-Hill Companies.)

Geoergescu-Roegen's view of the economic process leads to radically different conclusions than those of traditional free market economics. First, capital and resources are not substitutes, but complements. Agents of transformation cannot create the materials they transform or the materials out of which they are made. Further, Georgescu-Roegen questioned how long economic growth, fueled by energy from nonrenewable resources, could last. Analytically, Georgescu-Roegen expressed it this way:

> *Let S denote the present stock of terrestrial low entropy and let r be some average annual amount of depletion. If we abstract (as we can safely do here) from the slow degradation of S, the theoretical maximum number of years until the complete exhaustion of that stock is S/r. This is also the number of years until the industrial phase in the evolution of mankind will forcibly come to its end. Given the fantastic disproportion between S and the flow of solar energy that reaches the globe annually, it is beyond question that, even with a very parsimonious use of S, the industrial phase of man's evolution will end long before the sun will cease to shine.*
>
> (Georgescu-Roegen 1993:84–85)

13.3.2. Characteristics of Ecological Economics

The views of Georgescu-Roegen and others led to new ways of thinking about interactions between environmental and economic processes and to the growth of ***ecological economics*** as a distinct economic paradigm. Unlike traditional growth economics, ecological economics asserts that human-made capital cannot, in the long run, substitute for natural capital in providing raw materials and energy, stock (nonrenewable) resources, flow (renewable) resources, a sink for wastes, and key life support systems including water, air, climate regulation, food, and biodiversity. Thus, ecological economics sees the human economy not as a self-sufficient system that could draw material from or dump material into the environment without restraint, but as an environmentally dependent subsystem of human activity that would cease to function without environmental goods and services (Figure 13.11). In the past, the sense of independence was created because the human economy was small relative to the planetary biosphere and sources of raw materials and sinks for wastes were relatively large (Figure 13.11a). But as the human economy has grown, the source and sink regions of the biosphere have diminished due to use and degradation, and so have their capacities to provide resources and absorb waste (Figure 13.11b). In times present as well as in times past, traditional economists have often committed the error of thinking of "nature" or "the environment" as a subset of the human economy, a place from which to withdraw resources during production and a place to dump wastes after production was completed. In fact, the human economy, regardless of its past or present size and impact, will always be smaller than and contained within the physical environment, and is ultimately dependent on it in order to function. In this fundamental understanding is the first step toward both the economic and environmental sustainability that are necessary prerequisites for the conservation of biodiversity. And because the human economy must always be correctly perceived as a subset of the greater economy of the environment, the human economy must make environmental constraints a more explicit consideration in producing goods and services and disposing of the waste that such production creates (Costanza et al. 1997). Specifically, these constraints are manifested economically as:

1. Increasing capital costs of obtaining raw materials and energy when depletion occurs
2. Increasing inputs required to produce each output from the same capital due to diminishing economic returns (e.g., more fertilizer and pesticides may be needed for each yield unit in agriculture)
3. Increasing demand for more effective and expensive pollution prevention and clean-up (expressed as higher input costs or higher government or household expenditures)

Although the alternatives to growth economics are diverse, common threads among ecological economists are that economic activity should:

1. Be practiced on a sustainable scale
2. Use methods and practices of fair distribution of economic goods and services
3. Provide for efficient allocation of resources

In addition, systems of ecological economics require: (1) a redefinition of "growth" and a differentiation among types of growth; (2) an explicit determination of environmental constraints on economic growth; (3) definition of the functions of the environment in economic systems; (4) the creation and organization of markets for environmental goods and services, combined with methodologies for

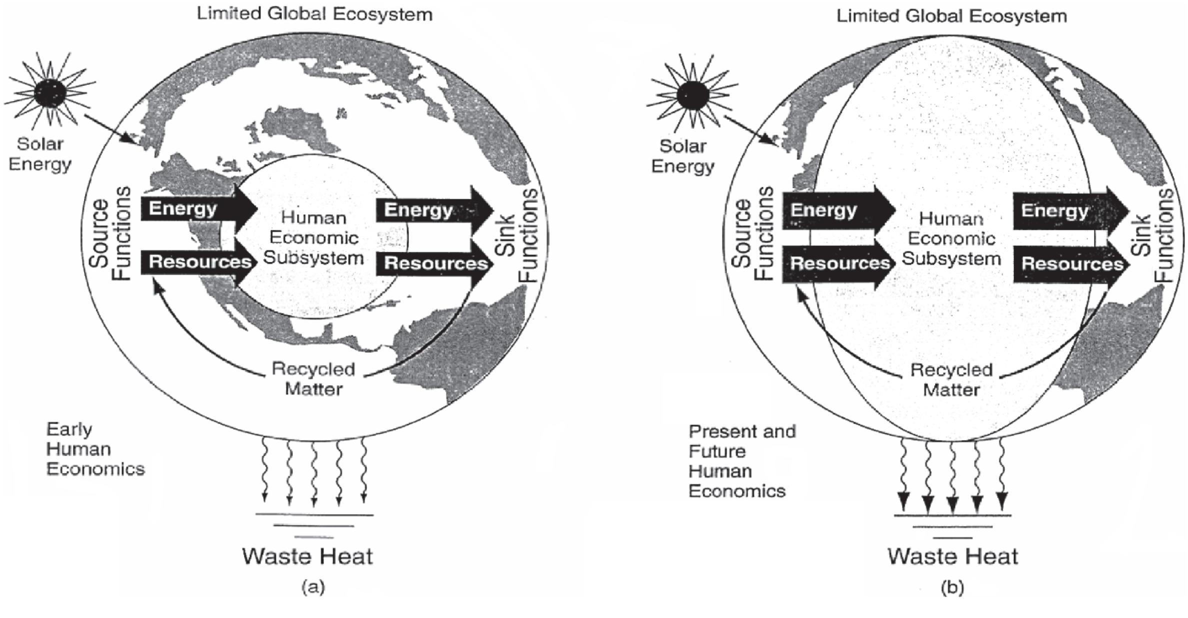

FIGURE 13.11. Schematic depiction of the relation between the economy and the environment. The environment provides raw materials and energy, stock (nonrenewable) resources, flow (renewable) resources, a sink for wastes, and key life support systems. In the past, the human economy was small relative to the biosphere and sources of raw materials and sinks for wastes were relatively large (a). As the human economy has grown, source and sink regions of the biosphere have diminished due to use and degradation, and so have their capacities to provide resources and absorb waste (b). (Fred Van Dyke, *Conservation Biology: Foundations, Concepts, Applications*, Copyright 2003, McGraw-Hill Publishers. Reprinted with permission of The McGraw-Hill Companies.)

valuing natural capital; and (5) alternative measures of human well being.

Years ago, when asked whether a newly-independent India would follow the British pattern of economic growth, Mahatma Gandhi replied, “It took Britain half the resources of the planet to achieve this prosperity. How many planets would a country like India require?” (quoted in Kainer et al. 2006:4). Armed with such insight, Gandhi would have understood why ecological economists Herman Daly and Kenneth Townsend called the term “sustainable growth” an “impossibility theorem” because “When something grows, it gets bigger. When something develops it gets different. The earth ecosystem develops (evolves), but it does not grow. Its subsystem, the economy, must stop growing, but it can continue to develop. The term “sustainable development” therefore makes sense for the economy, but only if it is understood as ‘development without growth’ – i.e., qualitative improvement of a physical economic base that is maintained in a steady state by a throughput of matter-energy that is within the regenerative and assimilative capacities of the ecosystem” (Daly and Townsend 1993:267).

Because confusion over “growth” and “development” is rampant when discussing the economy, ecological economists distinguish between three types of economic “growth”: (1) growth of biophysical throughput; (2) growth in production or income; and (3) growth of human welfare. “Throughput” refers to flows of matter and energy from the first stage of production through consumption. Growth in throughput is probably the most environmentally harmful, as it is characterized by high rates of consumption of matter and energy, relatively low efficiency of energy use, low durability and rapid replacement of material artifacts, and increasing rates of waste production.

Growth in production or income has the potential to be more environmentally benign. If increased production is characterized by more durable goods generated with less energy per effort, it may put less stress on environmental systems in the long run. “Income” is technically defined as *the flow of service through a period of time that is yielded by capital* (Daly 1991), but increases in income do not necessarily represent more material consumption and accumulation. Rather, they represent increases in “services” delivered and satisfaction with those services. Thus, it is theoretically possible for income to increase while environmental degradation decreases.

Growth in human welfare is at once the most important and most difficult to measure of the growth indices. Traditional free market economics has used per capita GNP or per capita GDP as its usual index, but ecoloigcal economists question whether either statistic measures human welfare. One alternative measure to per capita GNP is the Index of Sustainable Economic Welfare (ISEW), which integrates (1) income distribution (difference between the richest one-fifth of the population and the lower four-fifths); (2) net capital growth (measured as total net capital growth by adding increases to manufactured capital and subtracting the amount required to maintain the same per-capital level); (3) natural resource depletion and environmental damage (measured as the depreciation of natural capital by subtracting an estimate of the income lost to future generations by the current depletion of exhaustible resources such as fossil fuels and other minerals, as well as by the loss of biological resources, and adding estimates of environmental damage in the form of possible changes in climate, air and water pollution, and noise pollution); and (4) unpaid household labor. The ISEW also adds the value of expenditures on good streets and highways, public health, and education, and it subtracts defensive expenditures on health and education (e.g., trauma care and remedial reading programs), spending on national advertising (aimed at increasing demand), and costs of urbanization, commuting, and auto accidents. The ISEW is a dollar value that can be compared with per capita GNP, the traditional measure of economic well-being. Whereas the per capita GNP and GDP have continually increased in the United States and other industrialized countries, the ISEW has decreased in recent years (Figure 13.12).

13.3.3. Methods for Valuing Environmental Goods and Services

13.3.3.1. General Strategies

In conservation, a deficiency of traditional economics has been its failure to define markets for environmental goods and services, but markets remain powerful tools for determining value. One of the challenges of ecological economics is to create markets for environmental entities that did not previously exist. Properly developed, environmental markets stimulate market efficiency and improve overall economic efficiency, as well as support a higher level of biodiversity conservation. Environmental markets are most

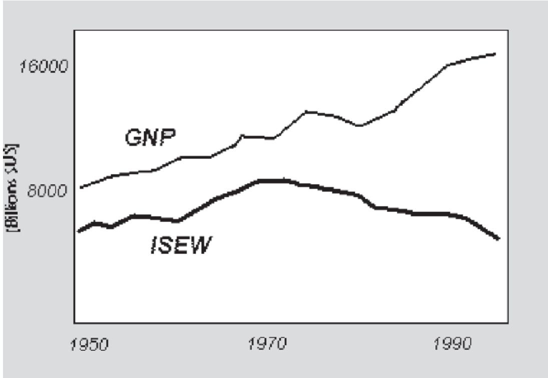

FIGURE 13.12. Changes in US Gross National Product (GNP) and ISEW (Index of Sustainable Economic Welfare) since 1970. Although GNP has increased, ISEW has begun to decline.

effective when they operate under one or more of the following three principles:

1. ***Polluter Pays Principle*** – Economic strategies force polluters (rather than society) to pay for the pollution they create and prevent them from externalizing pollution costs.
2. ***Precautionary Principle*** – If the environmental outcome of an economic activity is uncertain, one should err on the side of caution and place the burden of proof on the potential polluter to demonstrate that economic activity will not do irreversible harm.
3. ***Polluter Pays Precautionary Principle*** – If uncertainty exists regarding the effect of a proposed economic activity, make the polluter pay in advance for the potential costs of remediation and restoration, with the investment returned if no pollution occurs.

13.3.3.2. Government Regulation

Government regulation is not, in the strict sense, a market mechanism for valuing the environment. Rather, it is an attempt to correct market failures when markets do not value the environment appropriately or efficiently. Through coercion and mandatory regulations, the government may require individuals or businesses to meet environmental standards they would otherwise disregard as uneconomical. Government regulations provide a minimum acceptable level of environmental protection for consumers and the public, but precisely because they are a non-market solution, regulations have significant weaknesses. For example, the burden of proof lies with the government to demonstrate that an environmental regulation has been violated, and proving such cases can be difficult and expensive. Thus, regulation encourages a "cops and robbers" mentality between regulators and potential polluters, often producing at best, reluctantly minimal compliance and, at worst, covert noncompliance. Enforcing regulations effectively is expensive. Enforcing regulations ineffectively is less expensive, but generates high levels of noncompliance, and defeats the purpose of the regulation. Additionally, regulation ensures that environmental concerns remain outside market culture.

Regulation also has benefits. The impetus of regulation has spurred innovation in pollution reduction technologies, effectively creating a "market" for pollution abatement devices where none previously existed. For example, regulations imposed on the US auto industry by the Clean Air Act led to rapid technological developments in automobile technology, such as catylitic converters, unleaded gasoline, more fuel-efficient engines, hybrid autos, and, eventually, electric and hydrogen-powered cars.

Regulation has historical precedent. Most of the early environmental legislation in the US, and later in other countries, initially took the form of mandatory regulations imposed by the government. The US National Environmental Policy Act, the Clean Water Act, the Clean Air Act, and the Endangered Species Act all derive their authority from the ability to regulate individual and corporate behavior according to objective, pre-set standards, and to impose fines or imprisonment for failure to comply. Interestingly, these acts have been successful mostly because of their requirements for information, rather than their threats of penalties. All require full disclosure of facts regarding individuals or businesses engaged in activities covered by legislation, so that the public, the press, the courts, and legislatures can evaluate them. In a society blessed with a free press, it is this public access to information that has done more to create compliance with environmental laws than the actual threat of penalty (Quinn and Quinn 2000).

To avoid some of the problems associated with mandated programs and regulations, governments may adopt and promote regulation through voluntary programs that provide information, technical assistance, and cash and material subsidies to encourage compliance. Voluntary programs reduce or eliminate the costs of enforcement and tend to create more favorable relations between government regulators and private enterprise. The major disadvantage of voluntary programs is that they may require heavier tax burdens to operate and thus result in what economists call ***deadweight social losses*** or distortions in economic efficiency and market function caused by the diversion of earned income to the government through taxes. For example, increased taxes on income usually lead to reduced demand for consumer goods and reduced production of such goods. In this case, the reduction in demand is not real, but is rather a "deadweight loss" imposed on economic activity by the government through taxation. Nevertheless, voluntary programs are economically more efficient than mandatory ones if the tax revenues needed to support the voluntary program are low *and* the costs of government services relative to the private cost of the same services are low, *or* if the voluntary program costs less than the mandatory program, or both (Wu and Babcock 1999). In general, voluntary programs are most cost-efficient when the number of individuals or businesses involved is large relative to the total population, and the government services provide nonrival public goods such as information or technical assistance.

Voluntary and mandatory programs to address the same environmental concern are not necessarily mutually exclusive. Complementary voluntary programs and enforced mandatory programs can achieve high compliance and efficient economic results. In such a carrot-and-stick approach, the government provides subsidies, information, technical assistance, and material capital to those who comply, while punishing the non-compliant with fines, confiscation of property or capital, or even imprisonment.

13.3.3.3. Taxation and Subsidies

The first action by governments to curb pollution and protect the environment usually takes the form of mandatory regulations, followed soon after by voluntary programs. Taxation is normally the third step, although it sometimes is introduced concurrently with voluntary programs. Taxation imposed on undesirable activities, a more market-like strategy for environmental protection, follows the "polluter pays principle" and can be one of the best ways to correct market failure, especially when used to force a producer of pollution to assume the burden of otherwise external costs. Taxation is an especially appropriate and effective method for controlling pollutants that are widely dispersed because the government is the institution best equipped to address the large areas and numbers of people affected. For example, if the government taxes a power plant for the hydrogen sulfide emissions produced in generating electricity on a per unit basis, it accomplishes two things at once. First, the government is effectively reimbursing itself for the social costs of air pollution, including increased costs of health care (due to respiratory diseases caused or aggravated by the pollution), increased costs of property damage to the government's own public buildings, structures, and lands (from the effects of acid rain) and increased costs of preserving species, habitats, and ecosystems that may decline due to pollution. Second, the government creates an incentive for the pollution producer to reduce pollution on its own, since every unit reduction in pollution lowers cost and increases the margin of profit. Two indirect benefits often result from the second effect. First, pollution control becomes part of the intrinsic "organizational culture." Second, if the pollutants are material in nature and are removed by the producer prior to emission, taxation may open up new markets for the pollutants to be used in beneficial ways. For example, "scrubbers" in smokestacks remove pollutants created by coal burning and thereby accumulate a "sludge." Although harmful as an air pollutant, the sludge is high in sulfur and can, if appropriately applied, be used as a fertilizer to supply an important plant nutrient for crops. The Tennessee Valley Authority, one of the nation's largest producers of electrical power, now makes from $6 to $10 million annually by selling the sludge gathered from its scrubbers. The Indianapolis Power and Light Company is even planning to adjust its operating conditions to produce higher-quality sludge (Hoffman 2000).

Just as governments have programs to tax environmentally harmful behaviors, they also have multiple programs that do exactly the opposite, providing cash payments or other forms of remuneration for activities that cannot be environmentally sustained in the long term. Price supports in agriculture, for example, require cash payments to farmers when market prices fall below profitable levels. In the United States, the recently passed Freedom to Farm Act was designed to eliminate such subsidies, but major federal loans and subsidies for farmers have been approved in every year in which large harvests resulted in falling prices for corn and soybeans. Soil erosion rates, pesticide and fertilizer hazards, declines in native populations of plants and animals, and continued degradation of groundwater and surface water in intensively farmed areas indicate that much traditional corn and soybean farming is not sustainable, but loans and subsidies absorb farmers' losses and encourage such practices to continue.

A global carbon tax is as controversial a proposal as eliminating subsidies for unsustainable behavior, but perhaps even more necessary. Carbon dioxide emissions represent perhaps the single greatest threat to global climate stability. A tax on carbon emissions would internalize the cost of such emissions, which are currently external to the production process, but quite real in the form of increased worldwide temperatures and their unprofitable effects on crop yields, increased incidence of violent and unstable weather events, rising sea levels, and increased risk to biodiversity worldwide (Malcolm et al. 2006). As industries sought to lower production costs, one of their first priorities, under a carbon tax, would be to invest in technologies that reduce carbon emissions and increase efficiency of energy use, slowing the negative effects associated with global climate change. Such a tax would make reduction in carbon emissions part of "corporate culture" by making the reward for reduced emissions intrinsic to a company's profit and loss, or to a nation's GNP.

Governments could create a tax structure based on environmentally detrimental activities. The more an individual or business participated in these activities or purchased products associated with them, the greater their tax burden. For individuals, such taxes might take the form of higher sales taxes on less fuel-efficient cars, taxes on non-recyclable or non-biodegradable products, or taxes on home heating or cooling practices that produced high levels of pollution. For business and industry, there might be an expansion of existing taxes and fees on pollution and waste on a per unit basis.

POINTS OF ENGAGEMENT – QUESTION 3

Suppose that all manufacturers of consumer products were required to charge a deposit to their customers on the retail packaging materials in which the product was presented, and also were required to accept the packaging material back from consumers and to pay back their deposit. What effect would this have on: (1) the price of consumer goods; (2) the type and amount of packaging materials; and (3) the production process?

13.3.3.4. Environmental Property Rights

One approach creating property rights for the environment is to sell “pollution rights” on a per unit basis. Like taxation, provision of environmental property rights is a manifestation of the “polluter pays principle” through which the government sells “rights to pollute” on a per unit basis rather than taxing each unit produced. Typically, the government establishes some absolute standard for operation (e.g., an absolute maximum number of pollutants allowed or a minimum level of environmental quality), outside of which producers are not allowed to operate. Within the boundaries of the standard, any producer must pay, in advance, for each unit of pollution emitted. In effect, this method tacitly asserts that an ecological system, such as the atmosphere, has value through the services it delivers. To degrade environmental services through pollution represents a social cost, for which the polluter must pay. Before purchasing pollution rights, however, the polluter receives a reward, in the form of a cost reduction, if he successfully reduces pollution and therefore is able to operate with a reduced outlay of expense for pollution rights. An additional incentive is the transferability of pollution rights. If a polluter does not “use up” all his pollution rights (because of increased efficiency and cleaner production), he can sell them to another polluter. Cleaner producers gain an economic advantage, and “dirty” polluters must pay more up front or buy more rights to pollute.

Tradable permits force regulators to identify a maximum acceptable level of pollution or depletion that is ecologically sustainable. Once determined, regulators must distribute the rights to pollute in some fair manner so that the market can attain efficient allocation of permits through trading. Pollution rights can operate in a free market, but only after ecological and political boundaries have been established (Daly 1999).

13.3.3.5. Insurance Against Environmental Damage

Governments and private citizens can require persons or businesses that contract with them for goods and services to provide proof of insurance against environmental loss or degradation. This approach is based on the “precautionary principle” and works like ordinary insurance approaches, except that it is applied to the environment. For example, such insurance might stipulate that if the logging practices of a timber company cause sedimentation above specified levels in surrounding streams, the cost of rehabilitation will be paid by the insurance company. As in the case of car insurance, the premium paid by the individual or business will depend on their environmental record. Businesses with records of environmental abuse would pay higher premiums because they represent higher risk, whereas policyholders with records of environmental protection would represent lower risks and pay correspondingly lower premiums.

Although environmental insurance is still not widely used, its applications are increasing. In addition to traditional forms of insurance against environmental damage, many larger banks and other large lending institutions are increasingly careful to inspect the environmental record of a loan applicant especially for loans on projects with potential environmental effects. Applicants with poor environmental records increasingly are considered bad investment risks (Costanza et al. 1997).

A variation on traditional insurance policies against environmental damage is a practice called ***environmental insurance bonding***, or, alternatively, ***flexible assurance bonding*** (Costanza et al. 1997) which is based on what might be called the “polluter pays precautionary principle.” An individual performing work that has the potential for environmental harm puts up, in advance, a bond equal in value to the cost of repairing such harm, should it occur. The party for whom the work is done places the bond in an interest-bearing account where it remains until the work is completed. If the party performing the work keeps environmental damage and costs within previously specified limits (i.e. performs as well or better than expected in terms of environmental damage), the value of the bond, plus some of the interest, is returned. If not, the money is forfeited and the money is used to repair the damage to the environment, if possible.

Another expression of an insurance-based approach to environmental protection is manifested in the habitat conservation plans (HCPs), previously discussed in Chapter 3. Recall that in an HCP, a landowner agrees not to use some of his land commercially for the protection of an endangered species using his property. In return, the landowner receives the equivalent of a long-term contract (the “no-surprises” agreement) that guarantees (insures) against any additional future restrictions and regulations by the government. The typical length of the agreement is 100 years (Quinn and Quinn 2000). Note an important shift of focus illustrated by these various forms of environmental insurance. Whereas government regulations place the burden of proof on the public and the government (i.e., the polluter is presumed innocent unless a violation is documented), environmental insurance and environmental insurance bonding place the burden of proof on potential polluters. Now such potential polluters must make a financial pledge asserting that they will *not* pollute, and forfeit the value of their pledge if they fail to live up to prescribed agreements.

13.3.3.6. Empowering Stakeholder Interests

Another strategy governments can adopt to protect the environment is to empower the interests of private stakeholders against polluters. For example, government agencies and their officials may use their resources to arrange meetings among stakeholders with diverse environmental interests, and may, in some cases, serve as mediators or arbitrators of those interests. The government may serve as a clearinghouse of information for stakeholders, or provide legal counsel to private stakeholders when they are opposed by larger corporate stakeholders.

The strategy of empowering stakeholder interests can accomplish things by itself, but it is often most effective when it operates under the shadow of government regulation. That is, the government may encourage and empower private stakeholders to reach agreements about environmental protection on their own, but simultaneously inform the stakeholders that, if they are unable to reach an agreement among themselves, then the government will impose an agreement on them. This threat of government intervention is often an incentive for cooperation among otherwise adversarial interests. For example, in 1995, an agreement was reached among private stakeholders for a 30-year effort in the restoration of water quality and fisheries in San Francisco Bay. This agreement was signed into effect only hours before a deadline set by the US Environmental Protection Agency, after which the EPA would have imposed its own water quality plan under the authority of the Clean Water Act.

13.4. Protecting and Valuing Biodiversity in the Economy: Current Conditions

13.4.1. The Convention on Biological Diversity

The Convention on Biological Diversity (CBD) recognizes that biodiversity conservation can confer wealth and economic opportunity to those nations who are able to successfully manage it and define their rights to it. The CBD states that “The essential objectives of the CBD are the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources under the umbrella of sustainable development …”

The phrase “the fair and equitable sharing of the benefits arising out of the utilization of genetic resources …” is one that directly addresses the concerns of developing nations. Specifically, it reflects their concern that multinational corporations, based primarily in affluent northern countries, will take their biodiversity resources, especially genetic resources from plants and animals, and use them to generate enormous profit for themselves and their shareholders with no repayment to the country the resources came from. Taking this concern from the biological to the cultural level, southern developing countries also are concerned that such companies will take (i.e. “steal”) the traditional knowledge of indigenous peoples regarding the use of biological resources, especially plants and their derivatives, in medicinal application and use such traditional knowledge in industrial scale processes that will, again, bring them great profit with no compensation to the communities from which the knowledge originated. These are not hypothetical concerns. They have arisen out of a long history of exploitive behavior by western corporations toward the developing nations which supplied them with raw materials for their profits. The pharmaceutical company Eli Lily developed their drug, Vinblastine, from extracts of the rosy periwinkle (*Catharanthhus roseus*) (Figure 13.13), a plant indigenous to Madagascar. Used to treat Hodgkins’ disease, Vinblastine has had a 90% success rate against this ailment. Subsequently, Eli Lily developed the drug Vincristine from the same plant, and used it in the treatment of leukaemia, where it proved 60% effective. These drugs earned Lily US$200 million through 2005, of which 88% is estimated to be pure profit. Through 2000, not $1 of these revenues had been shared with the people of Madagascar or their government (Zerbe 2005).

The rosy periwinkle story is not unique. In fact, such practices are so common that developing nations have had to invent a word for it. They call it ***biopiracy***, an expression now used in an almost technical sense to describe the illegal obtaining of biological material. Biopiracy is a continuing concern and problem because biodiversity and its attributes, often referred to in international laws and treaties as ***non-human biological material*** or NHBM, especially genetic resources, are, like most natural resources, ***common pool goods*** with low excludability. As economist Margaret Polski explains, “Natural resources are common pool goods: one user’s consumption subtracts from the supply available for others yet the physical nature of the resource makes it difficult to exclude users. NHBMs are discrete living organisms in common pool resources

FIGURE 13.13. The rosy periwinkle (*Catharanthus roseus*) of Madagascar, a species whose derivatives have been used by the international drug company Eli Lily to successfully treat Hodgkins disease and leukemia, generating millions of dollars in profits, but with no direct repayment to the government or people of Madagascar, the country of its source. (Photo courtesy of US Fish and Wildlife Service.)

(CPRs) that are integral components. In other words, they are part of the value chain that produces and provides common pool resources, which in turn are part of the value chain that produces and provides biodiversity" (Polski 2005:546).

Human agents who go in search of NHBM are often referred to as ***bioprospectors***, because, like prospectors of former times who searched for hidden sources of gold or silver, bioprospectors go into little known areas hoping to find previously undiscovered biological material that can have applications of great profit. But not all bioprospectors are the same, and their differences entail different values of biodiversity, and require different arrangements to protect such value. There are fundamentally three types of bioprospectors who harvest NHBMs. These are knowledge creators, entrepreneurs, and collectors. While knowledge creators and entrepreneurs are concerned mainly with use values of biodiversity, collectors are concerned primarily with its exchange value. Thus, each conducts a common activity with distinct purposes (Table 13.5). Again, Polski draws out the differences.

> *Knowledge creators, such as shamans, teachers, and scientists, bioprospect to advance knowledge. In the process, they may create new knowledge, products, processes, or applications, create profitable products, and add to collections of NHBMs. … Entrepreneurs, like farmers, vendors, and biotechnologists, bioprospect for NHBMs to build businesses, which may be small, medium, or large scale enterprises organized inside or outside the country in which the resource is located. While their primary objectives are to survive and develop profitable products, in the process they may advance knowledge, solve problems, and develop new processes and applications.… Collectors have more limited purposes: they harvest specimens to expand their own collection or to sell to others. Their bioprospecting activities have a single and relatively static economic dimension – harvesting an NHBM for immediate consumption – whereas the bioprospecting activities of knowledge creators and entrepreneurs are multi-dimensional and involve static and dynamic economic activities.*
>
> (Polski 2005:547)

Table 13.5. Different types of bioprospections and their purposes.

Purpose	Knowledge Creator	Entrepreneur	Collector	Activity
Advance knowledge	Yes	Yes	No	Dynamic
Solve problems	Maybe	Yes	No	Dynamic
Create new products, processes, applications	Maybe	Yes	No	Dynamic
Develop profitable products	Maybe	Yes	No	Dynamic
Expand collection	Maybe	Maybe	Yes	Static
Sell specimens to others	No	Maybe	Yes	Static

Source: Polski (2005). Copyright 2005. With permission from Elsevier.

These differences in the types of bioprospectors help us to understand exactly what people and nations are trying to protect when they attempt to guard the value of their community, regional, or national biodiversity. At the end of the transformation process of an NHBM, there are three potentially separable economic goods: the original NHBM (commodity), new knowledge (idea), or a product, process, or application (invention). The commodity is a concern of all three, but especially the collector. Entrepreneurs are often primarily interested in products, processes, or inventions that can be derived from biological material. In contrast to both, knowledge creators are primarily interested in ideas that can create knowledge, although they almost always also have an eye for its application. As a commodity, the economic value of biodiversity is best protected by property rights laws. As an idea, process, invention, or application, biodiversity and its derivatives are best protected as intellectual property by copyright or patent laws. However, a still more deeply embedded problem is that access to copyright and patent protection is not equitably distributed. Even these mechanisms have favored exploitation of resources of developing countries by northern- and western-based multinational corporations. But other seeds of conflict are planted even more deeply.

13.4.2. Integrated Conservation and Development Projects as Government Strategies to Encourage Just Protection of National and Indigenous Biodiversity

13.4.2.1. General Considerations

Ever since the Brundtland Report (World Commission on Environment and Development 1987) and the Rio 1992 Earth Summit, conservation, especially in southern nations of the world, has been increasingly concerned with people, economics, and poverty. Both the Report and the Summit alleged that conservation would become a sustainable and permanent part of the global human enterprise only if poverty was alleviated.

There is much to support this line of thinking. Despite the already enormous consumption of the Earth's ecological output by human societies, more than one billion humans suffer, by clear and objective criteria, from malnutrition, poverty, and lack of safe drinking water, adequate shelter and warmth, and basic health services. In fact, almost all of the world's "hotspots" of biodiversity (Chapter 4) are found in countries where poverty is widespread, and conflicts between resources for conservation and resources for human well-being take on increasing importance and urgency (Fisher and Christopher 2007). Worldwide, even if the human population were to be frozen at its present number, demands on the Earth's space and resources would increase. But the human population is not frozen; it is growing by more than 80,000 people each day, and stability is not expected until it reaches 10–12 billion.

There are four possible relationship categories between poverty and biodiversity conservation. (1) Poverty and conservation are separate and unrelated policy realms, with neither significantly affecting the other. (2) Poverty is a constraint on conservation. (3) Conservation should not compromise poverty reduction. (4) Poverty reduction depends on living resource conservation. Clearly the first option is not viable. Throughout the world, issues of conservation, poverty, and wealth are inextricably linked. According to the 2003 State of Food Insecurity (SOFI) report of the Food and Agriculture Organization (FAO) there are 842 million people considered 'food insecure.' Three-fourths of these live in rural areas, the majority in the developing world. As economists Brendan Fisher and Treg Christopher note, "The rural poor depend heavily on rural ecosystems for primary goods and services and therefore the importance of biodiversity to food security in the developing world cannot be overstated" (Fisher and Christopher 2007).

Currently 40% of the global population lives in low-income countries; roughly three billion people live on less than $2 a day, and 1.2 billion live below The World Bank's (2003) "extreme" poverty line of less than $1 per day. Conservation affects local livelihoods and local livelihoods affect conservation efforts. This "bi-directional" relationship can have positive feedback effects, often described as a 'vicious cycle' where "degradation and species loss affects local livelihoods in a negative way which leads to further degradation and so on …" (Fisher and Christopher 2007).

13.4.2.2. Serengeti National Park and Wildlife Harvests for Local Communities

Efforts toward sustainable development in recent years have increasingly emphasized the creation of ***integrated conservation and development projects*** (ICDPs) to ensure that conservation can proceed in an appropriate cultural context with sensitivity to human need. Typically, ICDPs include means through which local people share benefits of plant or animal resources in their environment at sustainable levels, take ownership of the conservation of such resources, and have an active role in decisions affecting the use and management of these resources in ways that benefit them individually and culturally.

An ICDP developed for the Serengeti National Park and surrounding environs incorporates wildlife harvest for local economies, individual subsistence to meet the needs of a growing population, and effective local enforcement procedures that discourage poaching and delay loss of biodiversity. Barrett and Arcese evaluated the plan with respect to a population model of the Serengeti wildebeest (*Connochaetes gnou* and *C. taurinus*) (Figure 13.14) herd. They determined that the number of wildebeest was

FIGURE 13.14. Wildebeest or gnu (*Connochaetes* spp.) are harvested by humans in the Serengeti of Africa and form an important part of the regional human economy, but current harvest rates cannot be sustained in the face of a growing human population. (Photo by Craig R. Sholley. Courtesy of African Wildlife Foundation.)

$$N_{t+1} = [N_t S_w^8 S_{dt}^4 + N_1 R_t] e^{u_t} - H_t$$

where N_t reflects the number of wildebeest at time t, S_w and S_{dt} are survivorship in the 8-month wet season and 4-month dry season, respectively, and R_t is the current recruitment rate. Losses are represented by harvest rate (H_t) of wildebeest by humans. Survival and recruitment rates are assumed to be functions of food availability, determined from separate functions (Barrett and Arcese 1998). Food availability is a function of area, grass production, and rainfall. An average household of seven consumes one-third wildebeest per year, leading to a regional take of 60,000 wildebeest annually.

Under their assumptions, the model predicted collapse of the wildebeest population in 9–14 years, and Barrett and Arcese concluded that wildebeest harvests could not be sustained at projected levels in the face of a growing human population (Barrett and Arcese 1998). In fact, the authors concluded that any ICDPs "that reduce essentially to game cropping are likely to collapse in less than one generation in the absence of other interventions to mitigate game meat demand and poaching" (Barrett and Arcese 1998). The model conservatively assumed human population growth rates of 3.4% or 3.9% and, not surprisingly, the wildebeest population collapsed faster when human population growth was more rapid. The plan's fundamental flaw was its failure to address endemic causes of rural poverty. Barrett and Arcese recommended that sustainable development and concurrent conservation would be best served if local agriculture were developed to be more profitable and more sustainable, thus reducing the need for wildlife harvests and the incentives for poaching. They suggest that "successful ICDPs will combat poverty, risk, and food insecurity by changing the capabilities and incentives facing human populations on parks' peripheries …" (Barrett and Arcese 1998).

In general, ICDPs involving wildlife harvests share three problems. First, while human populations are typically growing, the harvested wildlife populations often are not. Second, no wildlife harvest may be available during years of "environmental shock," such as drought, that reduce recruitment in wildlife populations to near zero, yet low recruitment in the wildlife population may coincide with periods of greatest human need, creating additional pressure on wildlife and initiating a spiral of population decline caused by having the heaviest harvests coincide with the lowest levels of recruitment. Finally, increased per capita income associated with development may lead to increased demand for wildlife products in very poor populations (Barrett and Arcese 1998).

13.4.2.3. Ecotourism as an Integration of Conservation and Development

Ecotourism has been defined by its own practitioners, such as the International Ecotourism Society, as "travel to natural areas that conserves the environment and sustains the well being of local people" (http:www.ecotourism.org/index2.php?what-is-ecotourism) (Figure 13.15). In particular, such activities that sustain "the well-being of local people" are usually identified with a specific form of ecotourism known as ***community-based ecotourism***, or CBET. As Agnes Kiss of The World Bank noted "… by the mid-1990s. USAID had 105 projects, totaling >US$2 billion, with ecotourism components …, and 32 of 55 World Bank-financed projects that supported Protected Areas (PAs) in Africa between 1988 and 2003 included a CBET component …" (Kiss 2004:232). CBET is attractive because it offers the prospect of linking conservation and local livelihoods, preserving biodiversity while simultaneously reducing rural poverty, and achieving both objectives on a sustainable (self-financing) basis (Kiss 2004).

We already have seen conservation efforts that included ecotourism, such as the Bonaire and Moheli Marine Reserves (Chapter 11), as well as in conservation efforts that integrate local community values into conservation efforts, such as A Rocha-Kenya's ASSETS program (Chapter 2). In Peru, communities participating in the Infierno Community Ecotourism Project have received approximately US$57,000 from revenues associated with shared ownership of the project with Rainforest Expeditions, an international tourism company, and US$60,000 in wages, both significant inputs to the income and employment of local families and their community economy (Kiss 2004).

Ecotourism can lead to the protection of biodiversity in one of two ways. In the best scenario, earnings from ecotourism are so high that local people give up all forms of destructive environmental labors or occupations and deliberately protect their environment to protect their new source of income. Alternatively, ecotourism can protect biodiversity if an outside group (business, NGO, or government agency) provides initial funds and capital to a community to develop ecotourism in exchange for the community's pledge to protect local biodiversity. In this scenario, money does not, at least initially, come from ecotourism revenues but from investment capital, given to community members on the expectation of future earnings.

FIGURE 13.15. Community-based ecotourism (CBET) offers one hope for linking economic prosperity of local people in areas of high plant and animal biodiversity with ongoing protection and preservation of that biodiversity. (Photo courtesy of A Rocha International and A Rocha Kenya.)

This kind of linkage is more risky, since, if revenues fail to materialize, local residents may nevertheless consider the initial revenues an entitlement for protecting biodiversity that should continue whether successful ecotourism develops or not. In this case, if payments do not continue, local protection of biodiversity may be stopped. However, this second approach can be very effective if properly managed. For example, the Amboseli Community Wildlife Tourism Project in Kenya pays a "land holding rental" as soon as a village agrees to dedicate an area of land for wildlife tourism. This rental is expected to stop once the tourism begins to generate revenues, but few communities have been willing to set aside land without this initial direct payment. However, once engaged, most communities have been successful in protecting biodiversity and contributing to other conservation objectives, and have captured and benefited from increased revenues from ecotourism (Kiss 2004).

Ecotourism also can achieve biodiversity conservation on larger scales because, if it becomes embedded in the fabric of a national economy as a major source of revenue, it begins to influence national policy. One tourism lobby persuaded the government of Ecuador to resist efforts to open a biodiversity-rich site in that country to oil exploration (Wunder 2007). Today the government of Mozambique is establishing large conservation areas as a key element of its tourism development strategy (Kiss 2004).

Although ecotourism has its share of success stories, the possible outcomes and linkages between biodiversity and ecotourism are only one manifestation of an intensifying debate in the conservation community about the best ways to use economic incentives to achieve conservation objectives. Ecotourism is really just one form of payment for ecosystem services. In this case the service is biodiversity, and the amount and kind of payment is determined by the private preferences of affluent ecotourists. But preferences also can be expressed at national levels, such as through laws that protect endangered species, or even through international conventions, such as treaties that aim to restrict global carbon emissions. The question is: what form should such payments for these services take? ICDPs take the approach that, to succeed, conservation must become an intrinsic value of local human communities, and must be fully integrated into community economic structure. The community that succeeds in such integration will receive the direct benefit of the ecosystem services they have conserved, which will come to be seen as costly goods vital to their own welfare. But an alternative approach takes a more direct path to the solution. Why not make direct payments to individuals or local communities for protecting or restoring ecosystem services which benefit others, whether the local community has fully integrated the benefits and values or not? That question has sparked a vigorous debate that broadly revolves around these two kinds of approaches: "integrated conservation development projects" (ICDPs), of which CBET is one form, and ***performance payments***, in which money is given directly to individuals or communities for meeting specified conservation objectives. Which of these is the most effective way to achieve conservation goals?

13.4.3. The Broader Debate: Integrated Development or Direct Conservation Payments?

Almost all conservation efforts today could be described as "interventions" that attempt to save species or habitats by trying to change human behavior at some level. An ideal "conservation intervention" that leads to local communities achieving measurable conservation objectives should possess the following characteristics: (1) be relatively simple in the sense that they allow practitioners to focus their energy on a few activities with high probabilities of success; (2) achieve conservation objectives in both the short and the long term; (3) achieve conservation objectives at the scale of ecosystems; (4) provide clear, direct incentives for residents to actively protect habitat; (5) deter immigration; and (6) reduce the social and political conflicts over resource allocation that often endanger ecosystem survival (Ferraro 2001). Can traditional ICDPs do all these things? Conservation policy expert Paul Ferraro summarizes the problem with ICDPs in a few words. "Experience with development interventions over the last 4 decades indicates that simply raising standards of living and encouraging economic growth is a major undertaking in many countries.… Advocates of development-based conservation interventions propose a much more difficult task. They propose, in effect, to guide or control the development process so that specific behavioral changes will occur and precise conservation objectives will be achieved. They are attempting not only to affect change, but to control the precise evolution of the change" (Ferraro 2001:992).

One of the problems associated with the ICDP approach is the high level of uncertainty regarding outcomes. Even if the development effort succeeds, its conservation benefits may be unexpectedly elusive and its unintended consequences unfavorable for conservation. Even when successful, ICDPs are problematic to conservation because of disjunctures at temporal and spatial scales. Conservation needs are often urgent. Integrated economic-conservation development may take years to bear fruit. Conservation usually demands ecosystem-wide strategies to preserve habitat and populations. ICDPs are community-specific, and their sphere of influence and effect no greater than that of the community in which they reside. Some ICDPs do attempt to operate on a larger scale, and some try to move development forward at rapid rates, but as Ferraro points out, "When practitioners quickly introduce new technologies, markets, and attitudes at large scales, they spread their resources thinly over a large territory, thereby diluting or misdirecting their impact" (Ferraro 2001:992).

An alternative to the ICDP approach is the ***direct payment*** (DP) strategy, or ***payments for ecosystem services*** (PES) schemes. PES approaches are voluntary, conditional agreements between at least one "seller" and one "buyer" with regard to a well-defined ecosystem service or, less directly, to a land use presumed to produce that service (Wunder 2007). In contrast to integrated development approaches, PES strategies aim at short-term, sometimes immediate results, and can often achieve them because they combine clear performance indicators with explicit assumptions and informed consent of all parties. One category of PES schemes for conservation are various forms of ***international habitat reserve programs*** (IHRPs). An IHRP is "a system of institutional arrangements that facilitates conservation contracting through multiple actors and individuals or groups that supply ecosystem services. The contracts specify that the outside agents will make periodic performance payments to local actors if a targeted ecosystem remains intact or if target levels of wildlife are found in the ecosystem" (Ferraro 2001:994). For example, PES schemes might take the form of paying landowners for conserving existing forests for their value in carbon sequestration (Figure 13.16). As Swen Wunder of Brazil's Center for International Forestry Research puts it, "The core idea of PES is that external beneficiaries of environmental services make direct contractual quid pro quo payments to local landowners and land users in return for adopting land and resource uses that secure ecosystem conservation and restoration … this contingent conservation approach explicitly recognizes hard trade-offs and seeks to bridge conflicting interests by means of compensation" (Wunder 2007:49).

Some of the most effective direct-payment programs can be found in countries with well-developed government conservation structures. In Canada, the United States, and much of western Europe, federal governments provide financial incentives to farmers to keep land out of agricultural production or shift it to alternative uses, thereby reducing the supply of agricultural commodities and augmenting the supply of environmental services. In Europe, 14 nations spent an estimated $11 billion from 1993 to 1997 to divert over 20 million hectares of land into long-term set-aside and forestry contracts. In the United States, the Conservation Reserve Program spends about $1.5 billion annually on contracts for 12–15 million hectares, an area twice the size of all national and state wildlife refuges in the lower 48 states. Similarly, the US Wetland Reserve Program (WRP) provides for direct payments of subsidies to farmers who remove cropland from production in formerly wetland areas and then return the removed area to its original wetland state.

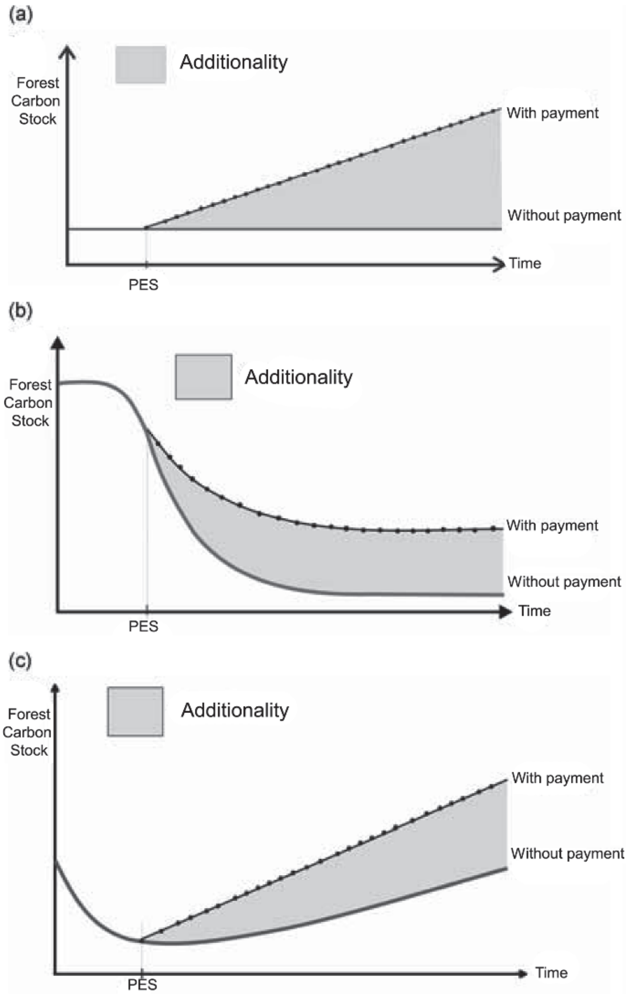

FIGURE 13.16. Three different payments for environmental services (PES) scenarios: (a) static, (b) deteriorating, and (c) improving service-delivery baseline. Dotted lines show de facto services delivered with PES; solid lines show counterfactual baseline without PES. Additionality (shaded regions) is the incremental service delivered through PES vis-á-vis the counterfactual baseline. (Wunder, The efficiency of payments for environmental services in tropical conservation. *Conservation Biology*, Copyright 2007 by Blackwell Publishing.)

A similar approach can work in developing countries. Using direct payments, practitioners can focus their scarce resources on two key tasks: the design of appropriate institutions and payment schemes. For example, Costa Ricans have created institutional mechanisms through which local, national, and international beneficiaries of ecosystem services compensate those who protect ecosystems. Costa Rica's Forestry Law (no. 7575) recognizes four ecosystem services: carbon fixation and sequestration, hydrological services, biodiversity protection, and scenic beauty. The law gives landowners opportunity to be compensated for provision of these services. Funds for the program come from the National Forestry Financial Fund, sources for which include fuel taxes and direct payments from other countries (e.g., Norway). The Fund establishes contracts for three management categories: reforestation, sustainable forest management, and forest preservation, with each receiving a fixed annual payment per hectare (Ferraro 2001).

Direct payments have some advantages over ICDPs. These are well-summarized by Ferraro.

> *With a smaller set of parameters to influence, practitioners are more likely to achieve their conservation objectives. They can be confident that if a contract is struck, the conservation effect will be positive. For large areas that include different agroeconomic zones, the complexity of using development-based interventions to promote habitat conservation is substantial. Practitioners must tailor supporting institutions and appropriate technologies to each zone. Using a contract approach, practitioners need only focus on variations in institutional arrangements across zones. Because performance payments can be targeted more precisely than development interventions, practitioners can be more confident that their interventions will have an effect on the areas targeted for conservation*".
>
> (Ferraro 2001:995)

But PES programs are far from perfect. In some cases, those enrolled take advantage of agency or NGO incentives, particularly in PES schemes centered on land use, by taking money for not doing something to the land that they never intended to do in the first place. For example, in the Costa Rican program previously discussed, Newburn et al. (2005:1417) note that, "In many cases, the costs of forest conversion exceeds the expected returns from alternative uses (pasture, agriculture), meaning these landowners have no intention of forest clearing during the contract period and the opportunity costs are effectively zero. The result may be that the Costa Rican government was allocating funds largely to protect forestlands that are not at immediate risk of deforestation." Some believe that the problems with PES run even deeper. Specifically, they fear that a PES approach, by delinking conservation from development, will deprive local communities in developing countries from their own legitimate aspirations for development of their own land and associated economies. That is, powerful and affluent conservation consortia will "buy off" local residents for relatively little money, preserving habitat and biodiversity but keeping local people at relatively low economic levels. A second concern, essentially the opposite of the first, is that paying people to be good conservationists and land stewards will erode traditional, culturally-rooted, not-for-profit conservation values historically held by the community (Wunder 2007). PES is not always the best strategy, but it may be "best suited to scenarios of moderate conservation opportunity costs on marginal lands and in settings with emerging, not-yet realized threats. Actors who represent credible threats to the environment will more likely receive PES than those already living in harmony with nature. A PES scheme can thus benefit both buyers and sellers while improving the resource base, but it is unlikely to fully replace other conservation instruments" (Wunder 2007).

13.5. Synthesis

Some conservationists, eager to make endangered species, critical habitats, and rare ecosystems able to stand toe-to-toe with industrial output, residential real estate development, and intensive agriculture, have developed or employed a variety of creative measures to document the dollar values of their concerns, while others, equally creative and passionate, have laid elaborate plans through which humanity can continue to take more but, through its increased ingenuity, degrade the environment less.

Both these approaches, although well intentioned and passionately advocated, have got the question backwards. The first because it fails to ask whether current systems of individual-preference market-driven valuations can ever rightly determine what is good for many, or how people will ever become better than their own self-centered appetites if those appetites are all that determine their economic behavior. The second errs because it sees human activity as an endless process of acquisition and degradation, progressively made more efficient to do less harm, but always doing harm nonetheless.

For conservation to succeed, conservation biologists must offer a different set of assumptions about economic behavior and a different array of questions. Specifically, how can we better choose what we shall value, instead of treating our appetites, wants, and desires as givens that must be satisfied regardless of environmental cost? And how can we restructure the human economic enterprise so that it not only ceases to degrade the world, but makes the human presence an agent of biodiversity conservation?

We can see, in individual communities and isolated efforts, that it is possible to make economic activity the reflection of value rather than the determinant of it, and it is possible to make human activity a restorative ecological force rather than an agent of ecological destruction. Today private economic incentives can aid conservation because social values have been changed, and that change has itself been shaped by laws and policies of the government that set certain environmental and conservation values, such as endangered species, wetlands, clean air and clean water, above and beyond market forces. Markets and property rights can be harnessed to achieve conservation goals when they are made to serve socially normative conservation values enforced by law and policy. But markets and property rights cannot intrinsically generate conservation value, and their historic failure to do so is an inarguable witness of the human experience. Conservation biologists, working with economists, must offer a careful and well-designed integration of conservation as an expression of human economic behavior that is guided toward conservation goals established outside of the economic process itself. And in doing so, conservation biologists must work to make conservation itself a normal pattern of economic behavior, not simply a series of heroic but ultimately futile, efforts to save things that no one ever really valued.

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14

On Becoming a Conservation Biologist: The Things Textbooks Never Tell You

> *It is never wise to seek prominence in a field whose routine chores do not interest you.*
>
> Eugene P. Wigner 1992

In this chapter you will learn about:

1. **The value of a personal mission statement in conservation biology and the principles for writing one**
2. **Elements in educational experiences and professional relationships that lay the foundation for opportunity and service in conservation biology**
3. **Objective criteria for selecting educational programs, mentors, and jobs in conservation biology**
4. **How to determine an appropriate stance on issues of advocacy in conservation as a conservation professional**

14.1. People as Agents of Conservation

When a celebrated alumna of a prestigious university was asked what she thought of her undergraduate training, she replied, "It was all very well done. Quite comprehensive. They taught me everything but how to get a job."

This lament is not unique to any particular field. In an effort to avoid appearing "vocational" or "prescriptive," colleges and universities often sidestep – at least in classes and textbooks – the issue of how people cease being students and become effective professionals in a particular vocation. Implicit in this silence is the assumption that ideas in textbooks will equip students to function at the forefront of their disciplines. The truth is, acquiring information about conservation is not the same as doing conservation. Textbooks do not perform conservation; people do. And the people who accomplish the most are those who become conservationists. Conservation as a career merits attention alongside conservation biology as an academic pursuit.

What follows is an unconventional chapter on the problem of moving from knowledge *about* conservation biology to effective involvement *in* conservation biology. For those who are now considering or committed to a career in conservation biology, your current and future education forms a vital role in that preparation. A fundamental question of that education is: what does a conservation biologist have to know and what does a conservation biologist have to be able to do? But before these questions can be answered, there are more fundamental and personal ones that must be addressed.

14.2. Conservation Biology as Vocation

14.2.1. Articulating Your Personal Mission in Conservation

Yogi Berra, the colorful ex-baseball player, once remarked, "If you don't know where you're going, you'll probably end up someplace." Unfortunately, "someplace" is not a very satisfactory destination. Having a clear understanding of one's own mission and purpose is an essential first step toward the kind of self-mastery that produces meaningful success and professional effectiveness. Clarifying a personal mission makes one's motivations clear and explicit, enabling internal restatement of motivations or explanation to others at any time and under any circumstances. Clarity of mission produces perseverance through discouraging circumstances and events. The act of writing a personal mission statement, or statement of purpose, also helps define not only one's mission, but also one's sense of *self* – an identity that exists independently of performance or external evaluation. This kind of self-knowledge provides the confidence to try new, unorthodox ways of accomplishing meaningful goals, the resilience to cope with setbacks and loss, and the freedom to fail and learn from one's failure.

An effective, personal understanding of purpose should be simple, clear, and memorable. Many students confuse a personal mission statement with the answer to the question, "What do I want to do with my life?" A personal mission statement does not tell you what to do. It points you in a productive direction to discover what you might be capable of doing, and why it might be meaningful to do it.

Although many students enter college with fundamental questions about what vocation to choose, and how to choose one, others think they already know, and move past the question of "What shall I do with my life?" to "How can I be most effective in the vocation I have chosen?" So, in conservation biology, many students who know that they want to be conservation biologists may want to frame their personal mission statements in more specific ways. To do so, one must identify the essential qualities of his or her role in conservation biology *without which a career in the field would not be satisfying*. For example, one student's motivations might lead to the following statement of purpose: "I want to work for an organization that deals directly with the management and conservation of endangered species." Such a statement is probably broad enough to allow the individual to consider both government and non-governmental organizations at national and international levels, but specific enough to limit and discipline his inquiries and preparations for such a career. Without that specificity, students can become overwhelmed and confused by the variety of possible preparations they could undertake, or the variety of organizations that are connected to the work of conservation. If you are serious enough to consider pursuing a career in conservation biology, be just as serious in defining your mission in conservation biology. Take the time to write down or type your personal mission statement. Reflect on it, revise it, and use it as a decision-making guide as you continue your work and study in conservation.

14.2.2. Pursuing Your Mission Through Education

In June 2007 the Society for Conservation Biology's official website (www.conbio.org) listed 420 academic programs in conservation biology being offered at 402 colleges and universities (SCB 2007). This is still a relatively small number of institutions in the global community of college education, but students are not excluded from the conservation field if they fail to graduate from one of these programs. Biologists engaged in conservation science today have earned their degrees in a variety of disciplines, including biology, ecology, environmental biology, wildlife management, fisheries management, botany, zoology, forestry, range management, and many others. When considering the curriculum that would best prepare you to be a conservation biologist, do what corporate business management guru Stephen Covey says, "Begin with the end in mind" (Covey 1989). That is, start with a clear idea of the goal, then form the best plan to reach it.

According to the Education Committee of the Society for Conservation Biology, the end that conservation biologists seek is to maintain three important aspects of life on Earth. These are: (1) the natural diversity found in living systems (biological diversity); (2) the structure, composition, and function of those systems (ecological integrity); and (3) and the resilience of these systems and their ability to endure over time (ecological health) (Trombulak et al. 2004). To complement this knowledge, a student also must be able to identify specific components of these systems, because these represent the specific elements to be preserved. Thus, courses in various aspects of biological taxonomy rank high in their educational importance in a curriculum of conservation biology. One needs to know how to tell the plants and animals apart.

With this kind of emphasis, the core of a conservation biology curriculum will need to provide a clear understanding of the biological and physical sciences and their ecological integration. The name of the program is less important than the actual courses taken to earn the degree. Attempts to define ideal undergraduate preparation for a career in conservation biology result in irresolvable debate; however, six components emerge as essential: (1) examination of basic biological processes and entities at cellular/genetic, organismal, population, and ecosystem levels; (2) training in mathematical analysis, interpretation, and presentation of complex sets of quantitative information, and practice in designing experiments to generate quantitative information; (3) studies of physical and chemical processes that govern basic biological processes and shape the external environment; (4) use of technologies widely applied in conservation; (5) consideration of the social, political, and cultural forces that shape the practice of conservation in human society; and (6) an understanding of management practices and applications to enhance natural biodiversity and mitigate threats against it at genetic, population, and landscape scales.

The fifth element must be part of a curriculum of conservation biology because, just as conservation biologists must understand how to maintain and protect the biodiversity of life on Earth, they must also be able to communicate the values and functions of that biodiversity to others. Therefore, courses that provide skills in communication, education, sociopolitical processes, and ethical and economic analysis are indispensable to effective function as a conservation biologist.

Finally, to have a complete perspective, a conservation biologist must understand the threats to biological diversity and know how to manage species and their environments in such a way that such threats can be mitigated or eliminated. As a curricular component, this means that specific, application-oriented courses, such as restoration ecology, ecological applications, conservation biology, or management-oriented courses in wildlife, fisheries, or range science add great value to one's education. Together, these ideas cover the major themes identified by the SCB's Education Committee (Trombulak et al. 2004) as the major education elements and goals of an education in conservation biology (Table 14.1). A curriculum that encompasses all of these components would be commendably ambitious, but hopelessly unrealistic if it tried to examine every area in depth. Students are wise to choose a particular emphasis, such as mathematical analysis, modeling, management application, conservation policy and regulation, or other focus, even as undergraduates, in order to have specific knowledge of one or more particular dimensions of conservation science. The current emphasis on interdisciplinary education should not obscure the need for intensive training in at least one keystone discipline. What conservation biology needs is not students who know a little about a lot, but students who have depth in a core discipline and sufficient breadth to converse with and contribute to other disciplines to achieve conservation goals.

Table 14.1. Themes and primary principles that should be used to guide choices and development of an undergraduate curriculum in conservation biology.

Themes	Primary Principles
Goals: the goals of conservation biology	Conservation biologists seek to maintain three important aspects of life on Earth: biological diversity, ecological integrity, and ecological health.
Values: why biological diversity, ecological integrity and ecological health are important	The conservation of nature is important for nature's intrinsic values, its instrumental values, and its psychological values.
Concepts: concepts for understanding biological diversity, ecological integrity, and ecological health	An understanding of conservation is based on key concepts in taxonomy, ecology, genetics, geography, and evolution.
Threats: threats to biological diversity, ecological integrity, and ecological health	Nature has faced and continues to face numerous threats from humans, including direct harvesting, habitat destruction, and introduction of non-native species.

Source: Adapted from Trombulak et al. (2004). Table format by M. J. Bigelow.

It is difficult to accomplish all these things during a 4-year undergraduate experience. Most conservation biologists working in the field today would admit to being "under-educated" (and some would confess that they were completely uneducated) in at least some of the categories of knowledge and skill that they now use daily. Yet they function effectively as conservation professionals because they acquired the missing components through graduate education, on-the-job experience, or by working as one member of a team of individuals with diverse expertise, each focusing on his or her own strength. If, upon inspecting your curriculum, you discover that some areas are not covered as thoroughly as others, there is no reason to panic. However, neither should you be complacent. Strive to take courses, either as requirements or as electives, that will develop your knowledge and competence in all of the above areas. But choosing the right courses is not enough. For an undergraduate experience to be truly effective, one must begin to take on the hidden hurdle of undergraduate education.

14.2.3. Making the Transition from Student to Colleague

14.2.3.1. The Hidden Hurdle of Higher Education: Attaining the Status of a Colleague

The lecture format is an efficient way of communicating large amounts of information quickly to a large audience of students. Unfortunately, lecturing rewards and reinforces all the wrong behaviors for success in the student's eventual working environment, a community of fellow professionals in which two-way communication is critical. As a student, you will not be able to avoid lectures. You may have heard many of them in this conservation biology course. But though the knowledge base of conservation biology is rooted in the natural sciences, human interaction is the primary process of achieving the mission of conservation. Because success in this mission is tied directly to interpersonal skills, every student must, at some point, recognize the need for these skills and begin to practice them. The transformation from being a recipient of information about conservation biology to becoming a contributing citizen of a professional community does not occur by accident, but by design. Through a series of intentional steps, you can develop the skills essential for the shift from student to practitioner, and, with similar intention, you can acquire experiences and credentials more substantive and distinctive than grades in courses. But first you must recognize what stands in the way.

Explicit hurdles for undergraduate students are passing courses and gaining a degree. For graduate students, it is the preparation of a thesis. For the new employee in the agency, it is meeting goals and targets. But lying beneath the surface of all three cultures is a similar hurdle – to attain the status of a colleague among one's associates. You cannot begin this effort too soon.

Earning good grades demonstrates that one has learned how to function successfully as a student. But graduate positions and jobs will require you to function much more independently in initiating programs, research efforts, and even organizational change with minimal direction. Performance in research and vocational positions during undergraduate years will often be used as a determining factor in measuring whether an individual can handle these tasks, and in assessing whether someone has the potential to become a useful colleague.

Throughout the world, the best undergraduate programs in all sciences try to facilitate this transition by requiring undergraduates to participate in at least one intense research experience, normally in their senior year. Outstanding programs in conservation biology are no exception. Whether research experience is an explicit requirement or not, undergraduates should actively pursue it, beginning in their freshman year. Many opportunities for research experiences exist – research-intensive courses, research with institutional faculty and graduate students, research with faculty at other institutions, and research with independent agencies or research organizations.

Where available, students should give serious efforts to research-intensive courses built into the undergraduate program of study. Many programs include and require a course with a title such as Senior Thesis or Independent Research Effort. Student who enroll in such courses should invest diligently to make the research effort of the highest quality, as original an investigation as possible with a final product that is as near to publishable journal standards as can be achieved. If there is no such course in the curriculum, there may be advanced courses that require a literature review paper in a particular subject. Students should view these assignments as opportunities to accomplish two things. First, they represent opportunities to produce a permanent document that can be copied, read, and judged by future evaluators. Although a literature review paper in a particular course or a senior research thesis may never actually be published, if its quality demonstrates that the student can do publishable work, it may make a favorable and distinctive impression that grades alone cannot convey. Second, the effort of a research paper or thesis helps the student to clarify his or her own interests, and to be able to express these interests in terms of a knowledgeable discussion of recent developments in the field. Thus, when evaluators ask for a statement of research interests, the student who has prepared a senior thesis or professional literature review can speak with greater power and precision than a student who can express his ideas only in terms of vague preferences, and will be able to provide a sample of written work that shows their ability to communicate complex ideas. Even if you do not encounter opportunities to prepare such a work as a course requirement, you can take on such a project personally. For example, you might consult with a professor to design a literature review that the professor would find useful for his or her own research, and offer to provide the literature review for them. This approach creates an accountability structure, provides ongoing input from a professional perspective, and can help to build a long-term relationship of trust and respect. Although this kind of practice is good, also look for opportunities that are more than practice, the kinds of studies that will be published. Even as an undergraduate, you can find opportunities to publish if you look for them. Producing published work extends the value of your efforts to conservation biologists all over the world, and provides a permanent and accessible example of the quality of work you do, which can be used by others to determine your merits for other opportunities.

Faculty and graduate students at most colleges invariably are conducting individual research efforts. They often advertise for assistants. Wise undergraduates should respond enthusiastically, even if the positions are unpaid. However, many such positions are not advertised, but will be offered to students who have performed well in classes and fostered positive relationships with faculty and graduate assistants. Some positions may be initiated by students themselves by offering their services as volunteers to assist in ongoing research efforts. People who prove themselves reliable in these roles invariably find themselves being given greater responsibilities and opportunities because they progressively gain the trust of those with whom they work.

Attaining the status of a colleague begins with understanding that you must manage an array of relationships, not just an array of courses, projects, or data. The first step toward learning how to be a colleague is the deliberate initiation of relationships with your associates. For students, this means engaging professors in conversations that are not always oriented around the need to clarify (or complain about) a particular assignment, but rather are discussions of issues of mutual interest and concern. In the environment of a conservation organization or agency, it means initiating the same kinds of conversations with other workers, including superiors. Initiate relationships with others by venturing outside your own peer group, educational status, or employment level and addressing issues with them that are about their needs, not yours. This advice should not be interpreted as encouraging insincere concern or false friendship, or suggesting a conniving strategy of using others for advancement. Genuine interest you demonstrate in others and in their work lays the foundation for the second step, in which you strive to become a solution to others' problems and an asset in their efforts.

The demands of conservation biology in academic and professional settings make time a scarce resource. As you begin to understand what your professors or fellow workers are doing, you will begin to appreciate the difficulty of the problems they face. When you see the opportunity, offer yourself and your skills as a part of the solution to one of their problems. For instance, assist with the collection of data in the field or with transporting equipment to a field site. Help with the preparations for a class or lab exercise. From this foundation, begin to seek out opportunities to work for faculty as a teaching aid or research assistant. Graduate students should look for opportunities for collaborative research, presentation, and publication with faculty. And new employees in an agency should seek cooperative efforts among others that pursue common goals important to the agency's mission.

Not everyone will want to treat you like a colleague. Some professors will always prefer to dominate students whom they can control, rather than develop younger colleagues with whom they could one day collaborate. This is an unfortunate and short-sighted perspective, but one that is tragically common. Many key leaders in conservation today can recall the critical role of inspiring and supportive mentors in their development, and some would even say that the success of current conservation leaders should be measured by their success in advancing the careers of future leaders in the field (Dietz et al. 2004). Work with those who demonstrate this perspective. They are the kind of people who will treat you with respect and demonstrate an interest in helping you to grow from student or employee to colleague and associate.

14.2.3.2. The Role of Vocational Experience

In academic cultures, some students see their professional preparation in terms of fall and spring semesters, and their summers as "vacations." The high cost of college often demands summers of hard work at the best-paying job you can get, but summers also can offer the best opportunity for students to begin to gain the experience and credentials that will facilitate their transformation to citizens of a professional culture. Many conservation opportunities are unpaid or poorly paid, but there are many that pay very competitive salaries while providing the experiences and opportunities that can radically transform your vision, ability, and influence in making a difference in conservation. Summers offer students the chance to escape the boundaries of their local campus. Faculty who obtain grants at other colleges and universities may advertise widely for assistants. Such ads typically appear as posters placed on the departmental bulletin board, in the newsletters of professional organizations, and as notices on web sites. Some types of grants in the United States, such as those administered by the US National Science Foundation (NSF), may have required procedures and protocols for distribution and be posted at various types of internet "clearinghouses" such as the Research Experiences for Undergraduates (REU) program. These and similar grants are specifically targeted for undergraduates and may be funded for long-term research, permitting applications to be made year after year. Some conservation organizations, such as The Nature Conservancy have special summer programs specifically designed to employ students (www.nature.org/wherewework/), while others, like the Student Conservation Association focus on placing students in conservation positions (www.thesca.org/conservation_careers/). In a typical 4-year curriculum, an undergraduate will have three summers between enrollment and graduation. If each summer is used wisely, and complemented with experiences gained during the academic year, students can build an impressive array of accomplishments and credentials that mark them as distinctive applicants for jobs and graduate research. In fact, students can distinguish themselves based on what they do professionally much more effectively than by their grade point averages.

Using summers strategically, research and vocational training also may come through direct employment with a government conservation agency or non-governmental conservation organization. In the United States, agencies such as the National Park Service, the Forest Service, Bureau of Land Management, Fish and Wildlife Service, National Resource Conservation Service, and others hire thousands of undergraduates each summer for agency work. In many cases, the agencies have established specific programs for the professional development and training of undergraduates, often with the explicit intention of grooming successful participants for future employment with the agency. Most state and local government agencies have similar programs. In the United States, many private and public conservation organizations, such as Mount Desert Island National Laboratory, Savannah River Ecology Laboratory, and Konza Prairie, to name a few, also offer extensive programs of summer research experiences designed for undergraduates. These opportunities are often prominently displayed on the department bulletin board. Too few students pursue them. Consider two case histories that illustrate how to apply these principles.

14.2.3.3. Putting Principles into Practice – Two Examples of Student-to-Colleague Transitions

Sarah Bowdish (Figure 14.1) grew up on a farm in northeastern Iowa, and went to college at a small liberal arts institution in another part of the same state. During her freshman year, she developed an interest in conservation, but her college had no major in conservation biology. Sarah chose a closely related major, biology/environmental science, to pursue her goals. By her sophomore year, she had learned, through building relationships with her professors, of ongoing research on the effects of burning and mowing on native prairie plant communities and their associated communities of birds. With strong recommendations and a good academic record, Sarah gained a paid position as a research assistant on such a study at the DeSoto National Wildlife Refuge in Iowa. The work was difficult and demanding. She was in the field before sunrise to start bird surveys on different experimental treatments. When bird counts were finished by mid-morning, Sarah began intensive plant sampling that often kept her at work until sunset.

FIGURE 14.1. Sarah Bowdish, an undergraduate student whose involvement in tallgrass prairie research and management, combined with interest in environmental and conservation policy, created a record of accomplishment and a network of contacts that prepared her for graduate research.

Sarah's dedication, diligence, and increasing knowledge of the prairies at DeSoto did not go unnoticed by the Fish and Wildlife Service staff. Increasingly they consulted Sarah about plant and bird responses to the management treatments, and began to make use of her knowledge of specific sites. Sarah was asked to continue as an assistant for a second summer. During that year she co-authored progress reports, wrote grant proposals with her professor, and learned some of the nuances of working with and gaining grant support from agency administrators. By the end of her second summer of research, the quality of her work and management recommendations had so impressed the DeSoto staff that they arranged for Sarah to speak to members of the Society for Range Management (SRM) at their annual meeting in nearby Omaha, Nebraska, and brought the SRM members to the refuge to do it. Sarah's presentation to the SRM provided her with many new professional contacts, as well as many compliments from the Society's leaders and members.

Sarah then submitted her work for presentation at the Annual Meeting of The Wildlife Society, to be held that year in Austin, Texas. After review, Sarah's abstract was accepted. Impressed by her accomplishments, her college paid all expenses for her attendance. Her presentation was not only an important contribution to the meeting, but provided another opportunity to establish further professional contacts. During the academic year, Sarah attended two student conferences in Washington, DC on issues of environmental law and policy. She used her interpersonal skills to become a leader among student caucuses, and an effective and persuasive advocate for conservation with her own senators and congressmen.

By the end of Sarah's junior year, her contributions to conservation management and policy began to receive wider recognition. She won one of 75 Morris K. Udall Scholarships in Environmental Policy; a $5,000 national award given to undergraduate students who show promise of being able to make exceptional contributions to environmental policy issues. Upon completing her undergraduate education, Sarah accepted a graduate assistantship at the University of Oklahoma to study the effects of global climate change on plant communities in tallgrass prairies. Along with fieldwork in the state, she traveled to the Czech Republic for additional, more specialized studies in modeling and computer programming related to carbon reactions in plants and global climate change. Her interests in politics and her strong interpersonal skills were soon having a pronounced effect on her colleagues at Oklahoma. Within a year she had been elected a Senator to the Graduate Student Senate of the University and elected President of the University of Oklahoma Botanical Society. Over the following 2 years, Sarah earned a Master's of Science in Botany. In her own words, Sarah describes the value of her experiences this way.

> *My experiences at DeSoto were extremely valuable for preparing me for graduate school. It gave me instant credibility with my professors and peers because I had real experience conducting research, analyzing data, preparing documents for publication and presenting my work at professional scientific meetings. It also gave me the confidence I wouldn't have normally had because I had been through the entire process before. As an undergraduate, I knew I loved the subject area I was studying but I didn't have a good grasp of how I could use my knowledge in a practical way. My research at DeSoto helped me see what kind of impact I could have to the work of conservation biology and it motivated me to continue my professional development.*

Nathan DeJager (Figure 14.2) enrolled in the same liberal arts college as Sarah at about the same time. Although a gifted athlete in football and baseball, he had little to recommend him as a student or future scholar. Like Sarah, Nathan had grown up on a farm, in this case only a few miles from the college, and his interest in the land around him and its care led him to choose a major in biology and environmental science. Through personal contacts, Nathan's major professor learned that the local office of the Natural Resource Conservation Service (NRCS) wanted to hire a technician for the summer to help with the county's Conservation Reserve Program, a federal program that subsidizes farmers to take selected lands of high conservation value out of crop production. Although his academic credentials were not impressive, Nathan was given a chance to interview for the position. His knowledge of farming and of the local landscape and local farmers impressed the NRCS staff and Nathan was hired. He proved so skillful at persuading local farmers to convert farmland to native prairie and natural riparian habitat that after only a few weeks Nathan was placed in charge of the CRP program for the entire county. Over the course of the next two summers, Nathan enrolled nearly 400 additional acres in the conservation reserve program, assisted in the restoration of three wetland areas, and helped design mitigation measures for the construction of two new livestock facilities to reduce their pollution impacts. In addition to allowing Nathan to continue to administer the CRP program, his supervisors placed him on two additional agency working groups on water pollution and riparian habitat restoration.

FIGURE 14.2. Dr. Nathan De Jager, Ph.D., University of Minnesota (USA). As an undergraduate student, Nathan's summer experiences coordinating the Conservation Reserve Program in Sioux County, Iowa helped him learn techniques of prairie and wetland restoration, as well as how to write research and management grants to pay for local restoration efforts.

In the course of his work, Nathan discovered that his own college owned a farm within his county that qualified for the Conservation Reserve Program, and that it included an important local stream. He convinced the college administration to alter its traditional farming practices, convert a portion of the farm to native prairie and riparian vegetation, and then raised $7,000 in external grants from the Iowa Department of Agriculture and

Land Stewardship and from Pheasants Forever, a private conservation organization, to pay for the restoration. Under Nathan's supervision, the restoration made excellent progress in its first 2 years. After graduation, Nathan accepted a full-time job with the NRCS in Boone, Iowa, where he continued to work with habitat restoration through the conservation reserve program and was directly responsible for the restoration of over 400 acres of wetland and associated upland habitat in his first 6 months. Following this effort, Nathan earned a Ph.D. in conservation biology at the University of Minnesota (USA).

Nathan described the value of his experience this way.

> *Working with the NRCS as an undergraduate opened my eyes to the "potential" native ecosystems in my own back yard. At the time, I probably knew more about tropical forests than native prairies. But when you grow up in the Midwest, where your back yard is 99.9% corn and soybeans, it is difficult to envision what the landscape once was or the potential such land has. What I took from my practical experience restoring native grasslands was an ability to see a landscape not simply for what it is today, but instead what it was, what it could be, and how to restore such landscapes. But I also learned that we are only beginning to comprehend how native ecosystems function, let alone restored systems. With a better understanding of how these systems work, restoration projects such as those I worked on can be more successful, probably cost less in the long-term, and provide the intended benefits. But without my work at the NRCS I doubt that I would have the ability to see the potential in degraded systems or know how to restore them.*

14.2.3.4. Common Threads in Different Cases – Successful Transitions from Conservation Students to Conservation Professionals

Sarah and Nathan had different stories, hopes, skills, and ambitions, but both made a successful transition from student to colleague. Both have made contributions to conservation entirely on their own merits by following four practices that any student of conservation could emulate.

1. As undergraduates, Sarah and Nathan used their summers to become involved in conservation practice.
2. Sarah and Nathan used interpersonal skills and technical knowledge to build trust, establish cooperative relationships, and persuade both scientists and the public to change practices and behaviors in ways that were of benefit to conservation goals.
3. Sarah and Nathan set out clear personal conservation missions and pursued them through personal initiative. For example, Nathan wanted to change agricultural practices in his local landscape to reduce soil erosion and preserve native prairie.
4. By making constructive contributions of value to their colleagues, Sarah and Nathan gained an increasingly wide network of contacts that expanded their influence, added to their credentials, and increased their effectiveness as professional conservationists.

Sarah and Nathan did not have the advantage of an explicit curriculum in conservation biology, nor did they enjoy the benefits of highly specialized courses or extensive institutional resources that are typical of large state universities. Both were first-generation college students whose families could offer them no special privileges or advantages in their chosen careers. Both eventually produced good, but not exceptional, academic records. But neither was "lucky." The achievements that Sarah and Nathan eventually gained were inevitable consequences of consistent, professional behavior, rightly applied to well-chosen ends through intelligent means.

POINTS OF ENGAGEMENT – QUESTION 1

What opportunities do you have in your current educational environment that can create the same kinds of outcomes that Sarah and Nathan achieved? What actions should you begin to take to transform these opportunities into tangible accomplishments and credentials?

14.3. Reaching a Wider Audience

14.3.1. Building a Professional Network of Contacts and References

People who want to work in any professional field, including conservation biology, must face some sobering statistics. In the total national employment of the United States, it is estimated that approximately 80% of all new positions are filled without ever being advertised. It has been estimated that the US national average percent success of an individual applicant in getting an advertised position is less than 7%. But when applicants have direct or secondary contact with the evaluator (i.e., one of the applicant's references knows the evaluator), the likelihood of success is estimated at 86% (Hart 1996). These statistics highlight the importance of *networking*. Why do networks make such a difference in success, and how does one use them effectively?

Every human being seeks satisfying personal and professional relationships. People tend to associate with others who are like them and share their fundamental values and goals. Through regular and repeated actions with one another, cooperation grows, and will increase even more among groups that share a common functional objective. Through regular interactions, and the consequent trust they establish, comes a foundation for permanent organizational success which benefits all individuals in the group.

Paradoxically, educational programs in most colleges that claim to prepare their students for professional success often fail to prepare them for these relational realities. The typical college curriculum in conservation biology or related subjects rewards (through grades) only student demonstrations of knowledge and technical ability. This reward system tells students that if they increase in knowledge and ability, they will gain more and more reward. Further, it leads students to believe that they will always be evaluated fairly relative to other individuals. Such a belief system can survive only in the confines of an academic classroom.

In vocational settings, knowledge and technical ability are primary determinants of success only in relatively low-level positions with fixed tasks and deterministic job descriptions involving management of data and information. Higher-level positions require increasing skill, not only at managing data, but at managing relationships. Management and networking expert W. E. Baker tells the story of a mythical manager, Bill, who suffered from the kind of occupational myopia "that restricted his field of vision to the technical part of his job. He didn't know that his ability to get the job hinged on his success in cultivating, maintaining, and mobilizing a vast array of relationships. He didn't realize that his success depended so much on people he didn't yet know. Because he didn't build relationships and get hooked into the network, Bill wasn't able to discover critical information, influence key decision makers, negotiate successfully, or implement his strategy. He didn't see the world as a network of relationships. … Oh, yes. You're probably wondering what happened to Bill. Well, he was fired" (Baker 1994:4).

Although Baker speaks from the world of business, interpersonal skills take on additional importance in conservation biology because social and political outcomes are necessary for conservation to occur. Thus, effective interactions with other individuals of diverse background and training are essential for success. Cannon et al. (1996) note "The human interaction processes critical to the work of conservation biology include sharing information, explaining ideas and values, listening to others, communicating a clear understanding of the opinions and feelings of others, and working together to solve problems, resolve disputes, and carry out action plans" (Cannon et al. 1996).

Despite the essential and urgent need for these kinds of skills, academic programs have been slow to make them an explicit part of the curriculum. Cannon et al. (1996) surveyed 298 graduate programs in conservation biology and closely related fields as well as 702 public and private organizations that employed conservation biologists. A majority of respondents in both groups identified seven key areas in which training was needed: (1) written and oral communications, (2) explaining science and values of biodiversity to the lay public, (3) group decision making, (4) interpersonal skills, (5) group planning, (6) leadership, and (7) advocacy. Despite the perceived need for high levels of training in all of these areas, few academic institutions and even fewer conservation organizations offered courses in human interaction skills. Sixty-four percent of graduate faculty respondents and 78% of organization respondents considered these areas to be as important or more important than scientific knowledge and technical skills (Figure 14.3). Yet there was a gap between the perceived need and desire for such skills and their actual offerings in conservation curricula in educational and professional settings (Tables 14.2 and 14.3). If this gap is not closed, academic course work in conservation will fail to equip students for success and effectiveness in real conservation efforts.

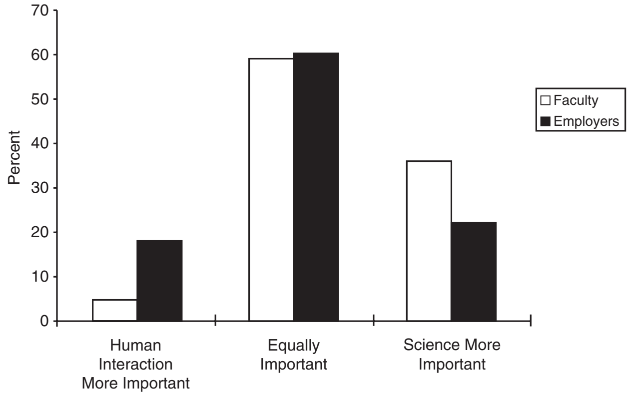

FIGURE 14.3. Employer and faculty ratings of the relative importance of science knowledge and skills compared with human interaction skills. (Cannon et al., Training conservation biologists in human interaction skills, *Conservation Biology*, Copyright 1996 by Blackwell Publishing.)

Such relational skills are essential in building effective professional networks, and networks are increasingly essential for professional success. As organizations grow in size and applicants grow in number, evaluators face ever more difficult decisions in selecting applicants for positions. More and more evaluators rely on their personal relations with other professionals, whom they do know, to make decisions about the selection of applicants, whom they do not know.

How does one form such contacts, and how does one judge whether or not a potential contact is a good one? Studies of human interactions reveal that people who work together toward common goals tend to form stable, positive, and mutually supportive relationships, even when personality differences are extreme. Thus, a first step in forming networks is to return to your personal mission, use it to identify goals of primary importance, find other individuals (in person or electronically) who share and are working toward these goals, and join them in mutually effective efforts. Joining and working in an organization in which members share a common mission is an effective beginning. To be successful, this will involve, at minimum, a commitment to attend the organization's meetings, participate in its discussions, hold membership in a committee or office, and contribute to work that defines the organization's purposes. In an electronic context, discussion and working groups abound that are defined by common interests and concerns for specific issues or problems. Conservation biology is

TABLE 14.2. Faculty ratings of training needs and current course offerings and requirements at academic institutions. For most categories, note the disparity between perceived need and course offerings.

	Perceived Need for Training (% of Respondents)				Courses Offered (% of Institutions)		Courses Required (% of Institutions)	
Skill Category	High (3)	Medium (2)	Low (1)	Average Rating	Yes	No	Yes	No
Written and oral communication skills	96.4	3.6	0.0	2.96	75.0	25.0	46.3	53.7
Explaining science and values of biodiversity to lay public	76.8	23.2	0.0	2.77	27.4	72.6	6.1	93.9
Group decision-making skills	68.7	26.5	4.8	2.64	38.1	61.9	10.8	89.2
Interpersonal skills	66.3	28.9	4.8	2.61	27.4	72.6	8.6	91.4
Group planning skills	64.2	30.9	4.9	2.59	33.3	66.7	8.5	91.5
Leadership skills	53.1	43.2	3.7	2.49	31.0	69.0	8.6	91.4
Advocacy skills	51.9	40.7	7.4	2.44	19.0	81.0	3.7	96.3
Negotiating or dispute-resolution skills	45.1	45.1	9.8	2.35	26.2	73.8	2.5	97.5
Knowledge of more than one language and culture	32.5	55.4	12.0	2.20	61.9	38.1	14.6	85.4
Interactive economic valuation skills	26.8	54.9	18.3	2.09	45.2	54.8	13.4	86.6
Interactive program evaluation skills	19.5	63.4	17.1	2.02	31.0	69.0	6.1	93.9

Source: Cannon et al., Training conservation biologists in human interaction skills, *Conservation Biology*, Copyright 1996 by Blackwell Publishing.

TABLE 14.3. Employer ratings of training needs and current course offerings and requirements at academic institutions. For most categories, note the disparity between perceived need and course offerings.

	Perceived Need for Training (% of Respondents)				Courses Offered (% of Institutions)		Courses Required (% of Institutions)	
Skill Category	High (3)	Medium (2)	Low (1)	Average Rating	Yes	No	Yes	No
Written and oral communication skills	90.4	8.8	0.8	2.90	20.0	80.0	27.5	72.5
Explaining science and values of biodiversity to lay public	75.2	24.0	0.8	2.74	11.8	88.2	17.6	82.4
Interpersonal skills	72.8	24.0	3.2	2.70	16.4	83.6	9.9	90.1
Leadership skills	65.6	32.8	1.6	2.64	19.1	80.9	9.9	90.1
Group decision-making skills	62.4	35.2	2.4	2.60	16.4	83.6	9.9	90.1
Group planning skills	55.6	41.9	2.4	2.53	14.5	85.5	11.0	89.0
Advocacy skills	56.9	32.5	10.6	2.46	10.9	89.1	14.3	85.7
Negotiating or dispute-resolution skills	45.6	44.0	10.4	2.35	13.6	86.4	5.5	94.5
Interactive economic valuation skills	29.4	50.0	20.6	2.09	1.8	98.2	8.8	91.2
Interactive program evaluation skills	22.8	54.5	22.8	2.00	7.3	92.7	8.8	91.2
Knowledge of more than one language and culture	16.4	45.1	38.5	1.78	1.8	98.2	4.4	95.6

Source: Cannon et al., Training conservation biologists in human interaction skills, *Conservation Biology*, Copyright 1996 by Blackwell Publishing.

no exception. By joining such groups and participating constructively in the work and discussion, relationships are formed that may mature into effective contacts.

While participation in organizations and in discussion and working groups is helpful in building an effective network, the most committed long-term relationships are likely to develop in more focused efforts, and often in employer–employee or mentor–student relationships. There are many opportunities for these to form. They may begin through mutual interest in the subject matter of a course, continue through common efforts in the discipline outside the course, and mature through the student's desire for guidance from the faculty member and the faculty member's desire to help the student. The circle of primary contacts will expand for students who actively pursue research and vocational experiences, especially experiences that lead them off their own campus to other colleges or outside agencies. The greater the diversity of experiences and organizations, the greater the number of primary contacts established.

Primary contacts can become "network partners" if they possess certain traits. A good network partner respects you, likes and understands you, and is involved and influential in an area related to your objective. Individuals who lack the third trait may be good and valued friends, but will be of little help in gaining employment or graduate education opportunities. Individuals who lack the first two qualities are potentially powerful but usually unhelpful. The presence of all three traits in one individual is what defines a person who will be most helpful in forming effective networks that lead you to discover opportunities in employment and education, and that can convince other people, whom you do not know, that you are worth their investment and risk.

14.3.2. Conservation as a Social Process: Involvement in Professional Societies

Like other humans, scientists are social. They form communities of common purpose, not only to achieve their purposes, but also to support and encourage one another emotionally to continue to strive toward those purposes. As Michael Soulé wrote about the origins of conservation biology, “Conservation biology began when a critical mass of people agreed that they were conservation biologists. There is something very social and very human about this realization” (Soulé 1985:3).

Once a professional society is formed, it soon has its own journals, conferences, bylaws, membership requirements, and certification standards. Although such societies are formed to advance a common mission shared by their members, they are also formed to provide personal and professional benefits to those members. There are many scientific societies engaged in various aspects of conservation, but the most identifiable and intentional of them is the Society for Conservation Biology (SCB). What does belonging to this society do for you and your development as a conservation biologist?

The SCB publishes two journals, *Conservation Biology* and *Conservation in Practice*, which all regular members receive. These journals serve to inform members not only of ongoing research in the discipline, but also, through their editorial policies that determine what will and will not be published in these journals, functionally define the agenda of conservation biology. Through editorials and commentaries, journals also serve to form, and inform, community-based views on conservation issues and values. This is not to suggest that a society’s journals can dictate what its members think. Anyone who has ever attended a faculty meeting or a professional conference knows that there is no environment more likely to produce disagreement than a room full of scholars. But despite appearances to the contrary, professional societies and their journals do function synergistically to shape a collective view of what a discipline is. In this way they provide members with professional identity, a function that is of great value to each person in further refining his or her own personal mission.

The SCB holds international, national and regional meetings at which its members can present the results of their research, meet one another, form associations of common goals and interest, and recognize and affirm significant accomplishments of individuals and the society. Such meetings also produce official organizational statements on important issues that allow the society to speak with a unified voice to the general public or to the political process.

Finally, the SCB maintains and makes available resources on jobs and graduate programs in conservation. The more members that are gainfully employed in conservation and the more satisfied they are with the value of their work, the more likely they are to remain active and productive members of the society. If such satisfaction erodes and is replaced by professional discontent, the society suffers.

It is valuable to visit the SCB website at http://conservationbiology.org to see how a collection of scientists with common mission and purpose present themselves socially to one another and to the world. Compare this presentation with other organizations that have related missions, such as The Wildlife Society or the Ecological Society of America, and note both the similarities and differences. If you wish to make your contributions to conservation maximally effective, you must express them in a social context of other professionals in some way and at some point. Without this dimension of professional life, even the best efforts are never fully effective. For some individuals, social contact is natural and easy. For others, it is uncomfortable and difficult. People who are shy or retiring by nature may find it easier to relate to others in activities focused around a common task or purpose, whereas naturally gregarious individuals may prefer purely social or recreational settings. Choose social interactions and contexts that you find most appropriate to your own temperament and interests, but do not neglect this dimension of professional life.

14.3.3. Integrating Education and Experience into Social Conservation Outreach

Ben Lowe (Figure 14.4) is no stranger to working intimately and effectively with diverse peoples and culture, starting with his own family. The eldest son of a US American father and a Chinese mother, Ben was raised in Singapore, speaking both Chinese and English from his earliest years. When his family moved to the United States and settled in Boston at the end of his high school education, Ben chose to attend a small liberal arts college, Wheaton College, in Illinois. Because of his interest in people and concern for the human condition, Ben originally planned to study in a major that would help him prepare for a career in overseas development, such as, perhaps, Political Science or International Relations. However, in his freshmen year, he found himself drawn to the subject and work in the college’s Environmental Studies program, and eventually settled on this as his major. Like Sarah and Nathan, Ben quickly realized the value of extra-curricular jobs and internships. At the end of his freshman year he secured a position as an Environmental Educator for The Audubon Society at one of their wetland preserves in Massachusetts, not far from his Boston home. The following year, now ready to spend the summer away, he worked on a National Science Foundation-funded study on the population dynamics of sea trout (*Cynoscion nebulosus*) along the Texas gulf coast at Texas A&M University-Corpus Christi. After his junior year, Ben obtained another NSF-funded position with a

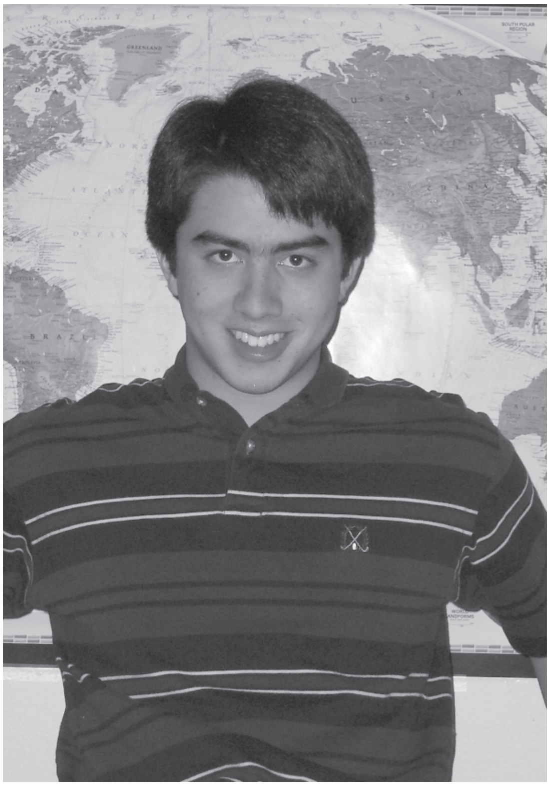

FIGURE 14.4. Ben Lowe, a recent graduate of Wheaton College (Illinois) who majored in Environmental Studies. Ben's combination of professional summer experiences in education, research, and development, and his careful development of a wide network of professional and scientific contacts helped prepare him to design and gain external funding to host a major student leadership conference on environmental conservation at his home college.

team of scientists working in Tanzania in Lake Victoria, studying the problems associated with sustainable fisheries for local residents. Although Ben had presented some of his work in traditional ways at an international scientific meeting, the Annual Benthic Ecology Meeting, during his junior year in college, he saw the need to translate conservation understanding, aims, and goals to a larger audience in order to make the work of conservation more effective. Beginning with his own peers, Ben formed the world's first student chapter of A Rocha, an international organization of Christians active in conservation (Chapter 2), at his home college. As his activism in environmental conservation increased, Ben realized that there were many colleges in the US and Canada, especially among smaller, Christian colleges, with little active student leadership in conservation issues. From his work in A Rocha, Ben had learned that large national and international organizations, including Conservation International, the National Wildlife Federation, and the United Nations Foundation, had established permanent staff, funding, and programs to assist faith-based groups and communities to take a more active role in conservation (Chapter 2). Drawing upon the already extensive network of professional contacts he had established in his first 3 years of college, Ben began writing and sending grant proposals to such organizations, and to the leadership of his own college, to support a conference he named The Wheaton Summit, designed to gather major national and international environmental and conservation leaders together with student leaders from colleges throughout the United States and Canada, and teach the student leaders how to become more effective conservation activists on their home campuses. Ben succeeded, raising over $18,000 in external grants to support the Summit, and persuading, among others, Sir John Houghton, former co-chair of the International Governmental Panel on Climate Change, to serve as the Keynote Speaker, with additional presentations by representatives from the United Nations Foundation, Conservation International, and the National Wildlife Federation. Ben's work came to fruition in February 2007, and the conference he helped plan and prepare with his fellow students was a great success.

Although stories like Ben's can initially be intimidating (one's first thought is, "I could never do all that!"), his story, like previous case histories, contains no element that cannot be imitated. If students are diligent to obtain job and internship experiences, continues to build their professional network, and, most importantly, takes personal responsibility for the state of things in their own environment, and then take action, they will succeed, although the forms of "success" will be different in every life and context. But no element of Ben Lowe's experience is outside the reach of any student who follows the same patterns and principles. Ben understood and pursued the goal of making the transition from a student to a colleague. Although that transition is not yet complete, Ben's determination to keep this goal foremost, and, as a result, to see himself as someone empowered to actualize his own goals, provided him with the motivation to pursue and attain significant conservation objectives, and to engage many people beyond his own campus to become part of an effective conservation effort.

14.4. Graduate Education in Conservation Biology

14.4.1. Independent Evaluation for Graduate School – The Graduate Record Exam

No matter how successful one might be in their undergraduate career, that career will come to an end, and one is then presented with the first major fork in the professional road – to enter the workforce or to continue education in graduate school. The best choice is determined by what is best for the individual who makes it. Graduate education is neither required nor essential for many kinds of conservation vocations, and it is neither the only nor the best path for every individual and every vocational mission. However, it is a road many take, and we will travel it first before returning to issues related to jobs and workplace decisions that are likely to affect all graduates, whatever degree or degrees they hold. For those who aspire to a graduate education, it is best to know *what* one is getting into, and *how* to get into it. To that end, we first take up the initial obstacle to pursuing a graduate education, a test called the Graduate Record Exam, or GRE, and the reasons for its importance in graduate school admission decisions.

Standards for grades vary among institutions, and high grades are more common, less distinctive, and less valuable than they once were. Recommendations, while important, are viewed by evaluators with some measure of distrust. References exaggerate. Sometimes they lie. Past cases of students suing professors over poor recommendations have tarnished the influence of such letters. Today students typically sign a waiver giving up the right to see letters of reference, but many references are still reluctant to put negative comments in writing. This leads to applications that often contain unfailingly positive, but mostly meaningless, recommendations. Records of employment and experience in conservation research and management are viewed favorably, but subjectively.

Contemporary evaluators face a dilemma. Grade reports, recommendations, and work evaluations are all valuable but subjective. They may be biased and distorted, and not easily comparable among applicants. Evaluators, particularly reviewers for applicants to graduate schools, have only one standardized measure that can be used as both an absolute and comparative standard – the Graduate Record Examination, or GRE.

The GRE is a standardized, multiple-choice test equally weighted in three areas of ability: analytical reasoning, math, and verbal. The analytical section tests the respondent's ability to think logically and draw conclusions or inferences from given information. The mathematical section tests mathematical and numerical skills and knowledge. The verbal section tests the extent of the applicant's vocabulary, skills in understanding the meaning of words and ability to interpret written expression of ideas. Answering every question correctly in any section receives a score of 800.

Perfect scores are rare, and even the best programs do not demand perfection. What constitutes an acceptable, or at least admissible, score for an applicant to a graduate program or a job varies. Some graduate programs have a defined minimum score, below which applicants will not be considered, regardless of the strength of credentials in other areas. Although there is no national standard, a common minimum is either a composite score of 1,800 or a minimum of at least 600 in each section.

Any student aspiring to graduate work in conservation biology must take the GRE. The most strategic time is to do so is in the spring of the junior year, the following summer, or, at the very latest, early in the fall of the senior year. If the scores are high enough on the first try, the student has this important credential in hand and can proceed with preparing other application materials. If the scores are not satisfactory, there is time to retake the test before most application deadlines pass. Although the GRE is promoted as an examination that tests the breadth of educational experience, and therefore not easily "studied for," most individuals can raise their scores on a second attempt, some significantly. Performance on the GRE improves with preparation and practice. Various GRE test preparation programs exist, ranging from free online preparation assistance to more intensive efforts via agencies that charge for their services.

14.4.2. Choosing a Program

Many students follow a path to graduate education to gain experience, knowledge, and credentials to better equip them to be effective and contributing conservation biologists. The first decisions are made in the application process itself because applicants should ask specific questions about each and every program they consider:

1. *Is its curriculum accredited by appropriate professional organizations?* For example, people with a particular interest in forest conservation biology can determine if their program is accredited by the Society of American Foresters, which maintains a list of schools with accredited curricula. Many other professional organizations with interests in conservation may accredit or in some way evaluate curricula.
2. *Do the faculty have a successful record of publication and grantsmanship?* Because a student graduating with an M.S. or Ph.D. in conservation biology or a related field will be judged not only on the degree itself but also on publications that result from his or her graduate work, it is wise to choose a program in which graduate theses and dissertations normally lead to one or more publications authored or co-authored by the student. In a quality program, this pattern is the rule, not the exception. In many programs, you can inspect the curriculum vitae of faculty members on line, determining not only their interests, but their productivity and success.
3. *Do graduate students in the program receive adequate financial support and other compensation?* Annual stipends vary by institution, but today are normally ranging from $10,000 to $16,000 for master's students and from $16,000 to $25,000 for Ph.D. candidates in conservation-related programs. Most waive or reduce tuition, and many provide health insurance. Although salary is not the only factor, it is generally unwise to commit to a graduate program that does not fund its graduate students. A lack of financial support, or of assistance in raising such support, means that the program has made

little meaningful commitment to or investment in its students' success.

4. *Do graduates of the program enjoy a good record of employment or placement in programs of more advanced graduate study?* Statistics on employment of graduates can usually be obtained from departmental or university records. A poor record of placement suggests that the program, and/or the work of its students, are not being perceived as credible by outside reviewers. A strong record not only indicates the opposite, but suggests that an incoming graduate student can gain access to a pre-existing network of supportive contacts who are successful graduates of the program.

Other program-specific factors are important, but sometimes more subjective and difficult to measure. Many things can be learned only by on-site visits and interviews. These personal contacts are essential to making a good decision. When meeting with faculty and students of the program in person, visiting applicants should try to determine how well the faculty and graduate students work with one another. Do they seem to enjoy one another, affirm one another's efforts and accomplishments, and work cooperatively in joint research and institutional efforts? An absence of these qualities, or, worse, evidence of personal hostilities among faculty or graduate students, identifiable "camps" or "followings," or negative comments about fellow faculty or students are symptoms of an unhealthy personal and professional environment that should be avoided.

14.4.3. Choosing a Project, Graduate Professor, and Mentor

Although the research project, graduate professor, and mentor are technically three different things, they are invariably related, and may all be tied to the same person. An ideal project is one the combines several traits. First, is the research of genuine interest to the student? Does the student want to have her name and reputation associated with this work in the professional community, and perhaps, in the eyes of the public? Although research interests will grow and expand in any healthy and developing career, it is likely that a student's name will be associated with his or her first publications for a very long time. Students should consider carefully if a proposed project is one that they respond to with enthusiasm, apathy, or dread. Poor fit between student interest and research effort leads to low levels of motivation, and that, in turn, leads invariably to poor research and low levels of subsequent professional success. Second, is the project of significant interest to the broader professional and scientific community? That is, does it address questions of foundational interest to the discipline, especially questions that, if answered, may provide general illumination on current theoretical or management predictions? Third, does the research address significant current issues or problems in conservation? Fourth, is the research doable within existing constraints of time, expertise, and funding? Doing good research is always challenging, but the probability of success should be significantly greater than zero. The practicality and "feasibility" of research will usually be evident if the student makes an analysis of proposed experimental designs, past successes (or failures), faculty expertise in the proposed effort, and background technical and logistic support for the project within the department and the university. Although some elements of a new project are always uncertain, projects that are overly doubtful are usually the product of poor planning and poor underlying support structures.

Although it is fashionable for academics and professionals to talk more about mentoring today than in the past, good mentors remain rare. The word ***mentor*** is derived from the Greek. It was not originally a word, but a name. When the Greek hero Odysseus departed for the war against Troy, he asked his most trusted friend, Mentor, to see to the education and training of his son, Telemachus. Out of this noble relationship and responsibility has grown the *definition* of what a mentor ought to be: "a trusted counselor or guide, a tutor or coach." Mentors are distinguished from teachers in that they are not merely interested in imparting knowledge and skills, but are actively interested in the total welfare and growth of the student or younger colleague. A true mentor possesses the wisdom to discern what is good for a student and has the power to bring it about. Thus, an ideal mentor is someone who takes a sincere and selfless interest in a student's welfare, sees his or her potential for growth as a person and a professional, understands what he or she needs to achieve such growth, and has sufficient personal and professional influence to arrange the resources and opportunities necessary to see that such growth takes place. Mentors also are distinguished by their efforts to train their students to make wise choices and avoid pitfalls that would slow their development. Students should be alert to the opportunity to develop relationships with true mentors and pursue them actively. There is no other single influence that can affect their future success as much.

14.4.4. Hidden Hurdles: The Problem of Traditional Approaches

Remarking on the state of academic scholarship in science in his own day, Aldo Leopold wrote, "There are men charged with the duty of examining the construction of the plants, animals, and soils which are the instruments of the great orchestra. These men are called professors. Each selects one instrument and spends his life taking it apart and describing its strings and sounding boards. The process of dismemberment is called research. The place for dismemberment is called a university" (Leopold 1966:162).

If Leopold's sarcasm is sharp here, he fashioned it so as a warning against the kind of over-specialized research of his own time that was of no use to conservation, and had no understanding of it. Unfortunately, despite such an eloquent admonition, there is often little evidence of real change in most graduate programs. One study of graduate educational training in the sciences that surveyed 4,114 doctoral students in 11 disciplines and 27 institutions found that 7 out of 10 believed they were well prepared to become independent researchers (Pérez 2005), but that is not the only, or, perhaps, even the best path to meaningful vocation in conservation biology. In another recent study, less than 20% of doctoral students in science disciplines thought they had sufficient training in workplace skills such as teamwork, collaboration, organization, and management (Gaff 2002). Two other studies which compared expectations of employers regarding the kinds of skills needed to be a successful professional scientist in conservation biology or entomology with the kinds of technical skills acquired during graduate school found that academically acquired skills accounted for only 7% of the total skill set that employers desired (Jacobson and McDuff 1998; Stanley and Higley 2000). Such findings have an uncomfortable consistency in their results But what do these results mean?

Although academic conservation biologists are in the business of education, they often appear to have little interest in the process of it. A survey of the work published in *Conservation Biology* by the journal's Education Editor, Carol Brewer, revealed that, while the number of papers on education has been increasing, it is still very low (Figure 14.5), with an average of only about four essays and research articles each year focused on this subject (Brewer 2006). In this regard, conservation biology is not different in its emphasis from other sciences. "Education," at advanced levels, usually means training graduate students to become scientific researchers, just like their professors. Unfortunately, as noted earlier, the actual work of conservation requires educating others, including the public, and demands high levels of communication, team building, leadership, and other non-technical human management skills. These kinds of skills are often ignored in a traditional graduate education in science.

We have seen that the hidden hurdle of an undergraduate education is to begin to make the transition from a student to a colleague. In graduate education, this remains an important hurdle. It is now more obvious, but also more specific in its implications. For the graduate student, the question is no longer exclusively "How do I become a colleague?" but, more importantly, "What kind of colleague shall I become?" This question must be asked openly and reflectively because, in graduate education programs in conservation biology, the educators will usually be scientific researchers with a narrow disciplinary focus. Not surprisingly, the faculty's "default setting" in such an environment will be to train their students to be imitations of themselves.

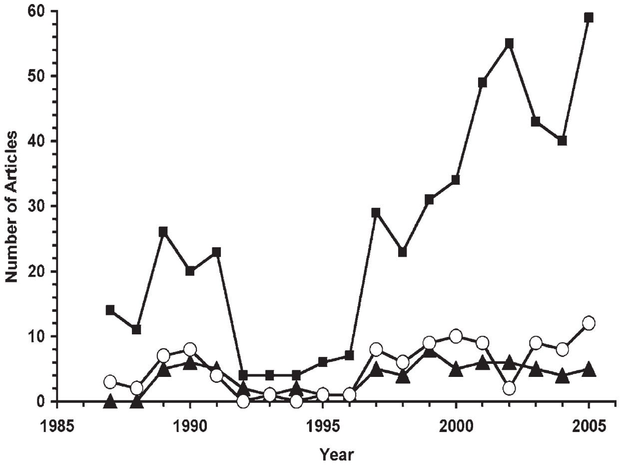

FIGURE 14.5. Numbers of contributed papers, essays, letters, and editorials published in *Conservation Biology* from 1987 to 2005 that include the words "education" or "outreach" (squares), the word "interdisciplinary research" (triangles), or that focus solely on education or outreach (open circles). (Brewer, Translating data into meaning: education in conservation biology, *Conservation Biology*, Copyright 2006 by Blackwell Publishing.)

There is nothing wrong with becoming a disciplinary researcher in conservation biology if that is indeed what one really wants to be. But that is not what everyone wants to be, and that is not the kind of approach that will solve every kind of conservation problem. Ironically, many of the same educators producing specialized researchers bemoan the failure of graduate education systems to produce more individuals with better management and human interaction skills, more interdisciplinary approaches and cross-disciplinary thinking, more creativity and problem–solution orientation, and more sensitivity to the complex needs of the increasingly global workplace environment. But one cannot keep doing the same thing over and over and expect a different result. Such behavior was, according to Albert Einstein, the very definition of insanity.

The problem with traditional graduate education is two-fold. First, it does not fit the aspirations or aptitudes of everyone. Second, disciplinary researchers cannot solve, or even identify, the array of problems that must be solved for the goals of conservation biology to succeed, and are therefore not fitted for many kinds of real conservation work with organizations that actually put conservation into practice. Conservation biologists Karen Kainer and her colleagues noted, in reference to real needs in conservation jobs, "As the workplace has become more interdisciplinary, global, and collaborative, … graduates are required to be technically proficient, broadly trained, and capable of working in teams. More than ever, there is also an emphasis on working toward a more humanistic and sustainable society, one in which the "academy" is obligated to generate knowledge and apply it to concrete problems …" (Kainer et al. 2006:4–5).

Given the state of things, it is not surprising that there are increasing calls both within and outside the community of conservation biology to not merely make minor adjustments in the educational process of training future conservation biologists, but to completely overhaul it. Such overhaul is still embryonic, but radical innovations are being attempted in some schools. Every student considering graduate education in conservation needs to be aware of these innovations, and to consider whether traditional or non-traditional approaches to graduate education in conservation biology are the right fit for their skills and goals. That is, every student must take personal responsibility to determine the kind of education, and the attendant projected educational outcomes, that are most consistent with their own personal mission and motivation. Otherwise, as a student, you may find yourself living out a career script written by someone else, and you may not like the part you have been given to play.

The narrowness of most graduate education programs and the attendant problems such narrowness produces have become so acute that the US National Science Foundation (NSF) developed a special program devoted exclusively to support more innovative efforts and educational approaches. This NSF program, known by the somewhat unwieldy name as the Integrated Graduate Education and Research Traineeship (IGERT), expresses an intention "to catalyze a cultural change in graduate education, for students, faculty, and institutions, by establishing innovative new models for graduate education and training in a fertile environment for collaborative research that transcends traditional disciplinary boundaries" (NSF 2005). IGERT funding has supported a number of innovative approaches to graduate training in the sciences, including conservation biology. The ones we review are examples, not an exhaustive list. But in studying their characteristics, you can gain a vision for the kinds of qualities and characteristics common to newer innovations in graduate educational approaches, and whether or not they might be better approaches for you.

14.4.5. Taking Interdisciplinary Study Seriously – Program Level Innovation in the University of Florida's Tropical Conservation and Development Program

In North America, the University of Florida has been long admired as an educational leader in conservation biology. However, despite that reputation, increasing faculty collaboration with scientists from other countries, particularly in Central and South America, revealed a growing frustration and disconnect between the formal graduate education students were receiving and the kinds of conservation problems they actually were being called upon to solve. Conservation problems, especially in developing countries, are not, strictly speaking, scientific problems, nor can they be solved by scientific investigation alone. Rather, such problems require engagement with economic motivators, social and cultural customs and practices, effective communication to non-science audiences, and the ability to lead and work with others in interdisciplinary teams. These skills were not being effectively addressed by traditional approaches to graduate education in conservation biology. "Conventional graduate training," noted Kainer and her colleagues, "related to tropical conservation and development has typically separated the two fields, with students focusing on either conservation from the perspective of the biophysical sciences or development as an extension of the social sciences.… Many graduates, however, find that on entering the workforce they are required to work beyond the boundaries of the discipline in which they were trained, addressing the complex interconnectivity between biological conservation and human well-being. Fundamentally, developing strong leadership from and for tropical regions is crucial for addressing this monumental challenge" (Kainer et al. 2006:4).

When old frameworks do not work, create new ones. So Karen Kainer and other faculty at the University of Florida did, forming the Tropical Conservation and Development (TCD) Program, attempting to devise an educational experience that could address theoretical, methodological, and practical challenges to tropical conservation and development. The TCD does not grant degrees but instead "… offers an interdisciplinary certificate that functions much like a minor. It also provides a supportive learning environment and fellowships and research grants for M.S. and Ph.D. students (enrolled in 20 participating academic units on campus) who are pursuing careers in tropical conservation and development.… Approximately one-half of all participants are from Latin America and other tropical countries, and many of these are supported with TCD fellowships. Between 1988 and 2005, the TCD fellowship competition had awarded 248 academic-year fellowships to 145 entering and continuing students from 27 countries" (Kainer et al. 2006:6).

So what do students in TCD actually do? Unlike traditional approaches, which tend to focus on independent research efforts, TCD students are required to engage in "practitioner experiences" in which they form a partnership with a host organization, such as a government conservation agency or national or international NGO. The student must learn about the host organization and understand its efforts and objectives sufficiently to reach the point of being able to complete tasks for the organization that advance its mission. Some examples of practitioner experiences include designing a forest inventory workshop for the local community, evaluating the environmental education program of an NGO, developing a GIS framework to assist an NGO in mapping an indigenous reserve, or, in interpersonal and leadership skills, organizing a workshop on conflict resolution for an NGO or agency staff.

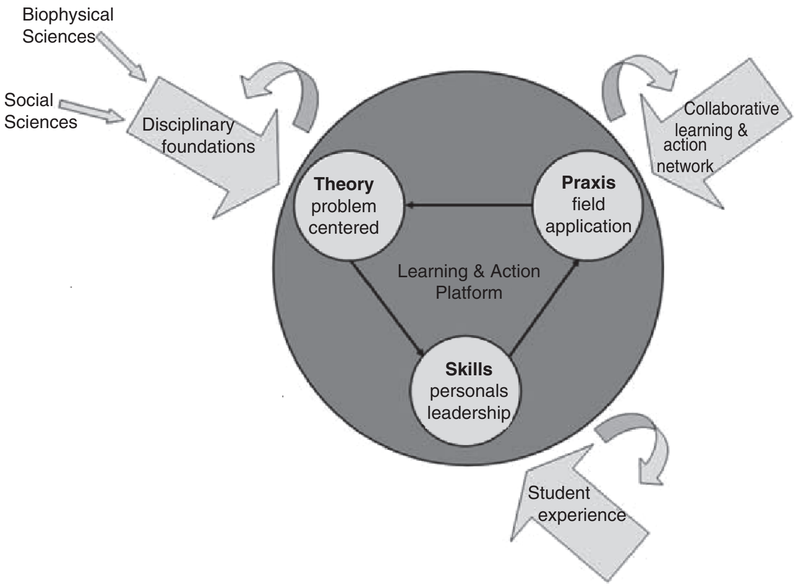

FIGURE 14.6. A conceptual depiction of the graduate education framework based on theory, skills, and practice used in the Tropical Conservation and Development Program of the University of Florida (USA). (Kainer et al., A graduate education framework for tropical conservation and development, *Conservation Biology*, Copyright 2006 by Blackwell Publishing.)

These kinds of practitioner experiences are designed to express the TCD learning and action platform, a three-legged stool of theory, skills, and "praxis," ("practice with reflection") (Vella 1995) (Figure 14.6). The practitioner experience and other dimensions of the program are expressed in three specific foci that intereact and suffuse all TCD graduate activities, which include training that (1) is problem centered, innovating across disciplines to focus on real world problems; (2) strengthens personal leadership, building on student experience and enhancing communication and critical self-reflection skills; and (3) converges in field application, linking graduate training and research to a collaborative network of others involved in the policies and practice of tropical conservation and development (Kainer et al. 2006:7).

Within the TCD program the emphasis is on developing other complementary skills critical for those working at the conservation and development interface: learn outside their immediate disciplines, think in terms of linked sociological systems, work in teams, negotiate among competing interests, communicate in nonacademic formats, and reflect critically on their own perspectives and actions. "The TCD platform of theory, skills, and praxis," noted Kainer et al., "creates an intellectual, social, and professionally safe space for students, faculty, and other TCD participants to creatively address the complex challenges of tropical conservation and development" (Kainer et al. 2006:8). In their evaluations, students affirmed that TCD provided them with opportunities to interact with and learn from professors and students outside of their home department (97%); provided courses that offered a balance between theory, applied knowledge, and skills (91%); helped improve their skills in communication (82%), critical thinking (86%), and understanding of the roles of scale and complexity in social and ecological systems (84%); helped them develop a research project that better reflected the realities of their research site (81%); contributed to their professional growth directly (89%); and provided contacts that would be a part of their professional network (88%) (Kainer et al. 2006).

14.4.6. Shifting the Scale: Innovative Approaches to Graduate Education in the Classroom

14.4.6.1. Legal Ecology 101: Integrating Conservation Management and Law

With similar emphasis on team building and interdisciplinary learning, and funding from IGERT, the Lewis and Clark University Law School in Portland, Oregon established a new course called Legal Ecology 101, Ecosystem Function and the Law, which has been team taught by Daniel Rohlf, an environmental attorney, and David Dobkin, an ecologist. Rohlf and Dobkin describe the course as one in which they "… take up to 20 students to a biological field station located on southeast Oregon's Malheur National Wildlife Refuge. Using the field station as our base of operations, we spend 4 (very) full days in the field exploring a variety of landscapes under the jurisdiction of different federal land management agencies; wetlands and shrubsteppe on national wildlife refuges managed by the US Fish and Wildlife Service, ponderosa-pine and mixed-conifer forests on national forests managed by the US Department of Agriculture Forest Service, and Great Basin high desert, juniper woodlands, and alpine tundra managed by the US Bureau of Land Management" (Rohlf and Dobkin 2005:1345).

Most classes in environmental law on Lewis and Clark's main campus, like most environmental law classes everywhere, focus on learning the laws and studying and memorizing court cases in which such laws are interpreted and applied. In contrast, in Legal Ecology 101, students learn in a field setting "… about legal and policy issues involved in managing these different areas and resources. Rather than emphasizing the details of environmental statutes and regulations, however, we concentrate on real-world application of federal land management schemes. For example, our course readings include the National Wildlife Refuge System Improvement Act, the organic legislation for the US wildlife refuge system passed by Congress in 1997. In the context of the course, we address this legislation and its mandate to maintain biological integrity, diversity, and environmental health by having the class meet for a discussion with the Malheur National Wildlife Refuge manager at refuge headquarters and then travel with a refuge biologist to various sites on the refuge to observe wetland management techniques and efforts to control exotic weeds and fishes" (Rohlf and Dobkin 2005:1345).

In addition to its field emphasis, Legal Ecology 101, like the TCD, also stresses the importance of working in teams and taking a problem–solution approach to conservation dilemmas. "During the final 2 days of the class," note Rohlf and Dobkin, "we ask participants to either evaluate or design selected elements of a landscape management plan that encompasses areas we visited during the week. For this exercise, we provide students with the actual federal agency documents and analyses. In 2003, for example, we asked designated groups of students to design a preferred alternative for a land-management plan addressing the Steens Mountain area, a task that the federal Bureau of Land Management (BLM) actually was working on at the same time" (Rohlf and Dobkin 2005:1346). In summarizing their experience of the course and the feedback and evaluations from students, Rohlf and Dobkin note, "Although it requires considerably more preparation, coordination, and logistical support than a typical classroom-based course in law school, we believe Legal Ecology has provided significant benefits – to the instructors as well as to the students. We have received overwhelmingly positive feedback from course participants. The hallmark characterization of the class by students has been relevance. Many students remarked that the class gave them a new perspective on environmental issues which we interpret as affirmation of interest in interdisciplinary approaches to both education and land management. Students interested in environmental law have been particularly enthusiastic about field instruction in basic principles of ecology. For some, the course provided epiphanal experiences, such as occurred one morning when we sat in a small riparian drainage discussing the complexities of a conservation agreement among federal, state, and private entities designed to benefit native redband trout (*Oncorhynchus mykiss* spp.) populations in this and several other area streams" (Rohlf and Dobkin 2005:1346).

14.4.6.2. Relational Skills in Conservation: Handling Humans, Learning Leadership

Believing that leadership is a skill that can be taught, not a gift that some lucky people are born with, Jeremy Martinich, Susan Solarz, and James Lyons of Washington, DC's American University designed an innovative educational experience for their students in conservation biology that stressed three elements: (1) a review and examination of the discipline; (2) exposure to and interaction with leaders in the field; and (3) a restoration project (Martinich et al. 2006:1579). The first element, review and examination of conservation biology, can be covered in a traditional classroom format. The second element involved numerous guest lectures by political leaders, executives of conservation NGOs, and heads of major federal environmental agencies, providing a wide array of perspectives that extend beyond traditional academic and scientific research. The third element, a restoration project, required the students to form five teams (Table 14.4), each with a different role in the project's completion. Each team had to succeed in order for the restoration to be successful. Some teams had an easier time completing their assignments than others. For example, of the continuity team, whose mission was to secure commitments of labor, infrastructure, and funding to bring the project to completion, the authors made this insightful comment: "After repeated trial and error the continuity team eventually learned not to ask for help, but rather to make clear how joining the effort would be beneficial to the stakeholder" (Martinich et al. 2006:1582). This is a valuable lesson, for it is one of the keys to understanding how to identify and speak to stakeholders and their interests in building conservation coalitions and broad-based support, an essential feature of ecosystem management (Chapter 12).

Martinich et al. concluded the explanation of their course with this appeal to their colleagues, "We urge conservation educators to incorporate career preparation into their conservation biology curricula in a way that allows students to gain a clearer sense of the interdisciplinary, challenging, laborious, and rewarding nature of conservation biology. We argue that the lessons and experiences gained by these students cannot be achieved without an implementation component" (Martinich et al. 2006:1582).

The course in conservation biology at American University made exposure to conservation leadership a key element of course instruction. Some have gone even further, making leadership qualities and skills the focus of an entire course. In the University of Maryland's

TABLE 14.4. A description of team responsibilities in a restoration project assigned in a project-based learning course at American University, Washington, D.C., USA.

Team Name	Team Responsibilities
Problem identification	Identify current biological, ecological, and socioeconomic problems at the site. Prioritize and select problems to be addressed in the management plan.
Design	Collect work products from other teams and determine how to craft a single plan from the variety of work.
Stakeholders	Identify stakeholders such as residents, industry, government, and advocacy organizations. Secure media coverage and financial support, equipment, labor, and expert advice.
Continuity	Secure commitments for labor (e.g., scout troops and church groups), infrastructure (i.e., support from local organizations), and funding (e.g., businesses and government to continue project in the future.
Implementation	Design implementation procedures. Manage work events and budget time. Acquire materials, tools, and any necessary permits.
Evaluation	Set standard of success and determine if project was successful in meeting goals. Create experimental design and manage all data collection/analysis.

Source: Martinich et al., Preparing students for conservation careers through project-based learning, *Conservation Biology*, Copyright 2006 by Blackwell Publishing.

TABLE 14.5. Questions asked of ten national and international leaders in conservation on issues of leadership by graduate students of the University of Maryland's (USA) Graduate Program in Sustainable Development and Conservation Biology.

Questions Asked of Ten National and International Leaders in Conservation
Why did you become involved in conservation?
What steps in your career were most important for developing your leadership skills?
Is a Ph.D. necessary for conservation leaders?
Were there specific role models who provided direction in your conservation thinking or activities?
What skills or characteristics are useful to leaders in conservation?
What leadership skills are necessary to direct a conservation organization or agency?
Are coalition building skills important to conservation leaders?
How did you deal with experiences that tested your skills as a leader?
Is it the task of a leader to pursue his or her own vision or the vision of the organization?
Does the conservation movement need a global leader, a Gandhi of conservation?

Source: Based on questions from Dietz et al. (2004). Table format by M. J. Bigelow.

(USA) Graduate Program in Sustainable Development, graduate students under the leadership of James Dietz took personal responsibility for their own education and coordinated in-depth, structured interviews with ten conservation leaders in federal and state government, academia, and conservation NGOs (Dietz et al. 2004). Their purpose was to attempt to define and understand common elements of experience, background, and perspective in these individuals that had contributed to their effectiveness and influence in conservation. Each leader was asked the same questions (Table 14.5), and their answers were recorded, studied, and analyzed. In learning about leaders' foundational motivations and interests in conservation, most leaders "identified childhood enjoyment of exploring nature as a primary factor influencing them to pursue a career in conservation biology. Several interviewees stated that an early interest in biology made for an easy transition to conservation biology" (Dietz et al. 2004:275). All ten leaders "acknowledged the value of interdisciplinary training in their career development. Even those who emphasized the need for grounding in a traditional discipline also identified the need for leaders to avoid "tunnel vision" and think about a variety of perspectives that different disciplines bring to a problem. Respondents also identified field experience in both ecology and policy as helpful in their professional development. Field work in biology was seen by some as the best way to understand both the ecological reality and the challenges facing conservation practitioners on the ground" (Dietz et al. 2004:275). Many identified the importance of inspirational mentors. Sometimes mentors were traditional academic scientists, but in many cases effective mentors were those who trained them in skills such as diplomacy, patience, and interpersonal relationships. Interviewees noted that the key qualities to be taught or modeled by leaders to leaders included passion or intensity of character, love for nature, ability to influence, inspire, and motivate others, persuasiveness, a knowledge base in science and/or policy, diplomacy, persistence, willingness to take risks, resiliency, ability to know when to compromise, integrity and consistency, and hope (not necessarily the same as optimism) (Dietz et al. 2004). Regarding their view of leading an agency, most of the respondents agreed that, in the words of Dietz and his colleagues, "… it is generally the leader's role to prioritize tasks and issues and to motivate the individuals to pursue organization goals … the leader must provide inspiration and guidance for his or her colleagues while allowing team members to find their own niche. The leader of a conservation organization was seen as someone who can match talent to tasks, develop trust among coworkers to become effective members of the team, and be ready to participate at all levels" (Dietz et al. 2004:276).

Overall, "Conservation leaders were seen as people with a clear vision of a large-scale action plan. They possess the interpersonal skills necessary to garner support within and outside their organization. They have a realistic view of what can and cannot be accomplished, and they strike compromise as necessary to keep the organization moving forward" (Dietz et al. 2004:277). More importantly, the kinds of questions asked of these leaders are the same kinds of questions everyone who aspires to leadership in conservation should ask themselves today, regardless of their current station or status.

14.4.6.3. Creating Your Own Path to Innovative Professional Development

Many colleges and universities do not yet have the kinds of institutional programs or courses that characterize the previous examples. When that is the case, taking personal responsibility and initiative is always better than complaint. Hector Pérez of the University of Hawaii did the former and, with the help of fellow graduate students, designed his own graduate conservation biology seminar on professional development. The purpose of the seminar was to learn how to develop nontechnical professional skills, like those displayed by conservation leaders in the course at American University, and often underemphasized in a traditional graduate education in science (Table 14.6). To do this, Pérez found speakers who represented various governmental and nongovernmental agencies, with each explaining their organization's role in conservation. Interestingly, Pérez recounts that "Every speaker emphasized the importance of possessing nontechnical professional skills. Skills such as conflict management, negotiation, strategic planning, lobbying, sociopolitical interaction, collaboration, human resources management, and fiscal management were common to each presentation" (Pérez 2005:2034). Pérez's proposal to graduate students in conservation biology to improve their professional development is simple. His advice is to create "… a professional development seminar series, guided by stakeholders in conservation biology, yet created by graduate students for graduate students" (Pérez 2005:2034).

TABLE 14.6. Some nontechnical skills essential for effective practice and leadership in conservation biology.

Professional Skill
Problem solving and evaluation
Sociopolitical interaction
Law, regulations, and policy analysis
Teamwork, conflict resolution, and negotiation
Public speaking and communication
Leadership, organizational management, and human resource management
Stakeholder and community relations
Marketing and social psychology
Strategic planning and project design
Economics and fundraising

Source: Pérez, What students can do to improve graduate education in conservation biology, *Conservation Biology*, Copyright 2005 by Blackwell Publishing.

But seminars are not the only venue for professional development. At national and local levels throughout the world, a variety of government agencies, conservation NGOs, professional scientific societies, and activist groups are vigorously engaged in the work of conservation. The pressures of taking courses, gathering data, writing a thesis, and, perhaps, serving as a course teaching assistant prompt an understandable and immediate reaction to involvement with these efforts. "I can't afford to invest the time." Perhaps one cannot afford not to. It might be best to choose venues to engage with the work and people of a particular conservation agency, professional society, NGO, or activist organization if you want these skills to be part of your educational experience. Without them, you might not get the kind of jobs that use them.

POINTS OF ENGAGEMENT – QUESTION 2

Suppose your own college offers no courses within your major that focus on learning nontechnical managerial and relational skills important to being effective as a conservation professional. Based on what you have learned from the preceding examples, what steps would you take to add these skills to your education?

14.5. Choosing a Vocational Setting

14.5.1. Should I Take This Job?

If you are a student now, it is vital to remember that graduate school is only one path to the goal of effective conservation work. And for all but those who become lifelong college professors, academic life is something that will not be the last stop in a career journey. Thus, one must consider what kind of vocational setting is appropriate to one's goals. In any vocation, the work environment is an important determinant of personal satisfaction and professional productivity. We sometimes have the luxury of choosing from several employment options. Location, salary, and benefits should receive their due consideration, but most people find that these are not the primary satisfying factors. For an emerging conservation biologist, other aspects are likely to exert a greater influence over personal satisfaction in work. Here are additional criteria to consider.

1. *Is there strong correspondence between the organization's mission and my own personal mission as a conservation biologist?* All effective organizations place definite limits on goals and priorities. Their effectiveness is, in large measure, a result of such limitations. By focusing on selected missions and targets for which they are uniquely suited, they achieve success. An important initial consideration, as a potential employee, is to look for alignment and correspondence between your mission and the organization's mission, between your interests and their interests, and between your abilities and their needs. The closer the match in mission, interest, and need, the more satisfying the work is likely to be, and the more you will be valued and esteemed by the organization. You also must consider the varying reward systems associated with different professional cultures and determine, in advance, what you want to be rewarded for and what you are good at producing that will gain rewards. For example, the reward systems of academic and non-academic careers in conservation biology are very different (Table 14.7). Academic researchers are rewarded for publication and grantsmanship, while conservation managers in non-academic settings, such as government, are rewarded for providing data to guide specific management actions and policies and doing it quickly. These different incentive and reward structures create very different professional cultures and working environments.
2. *Does the organization reach the same audience that I want to reach?* As in the previously discussed issues of scope in conferences and journals, so conservation agencies and organizations operate at international, national, regional and local levels. Is the sphere of influence in which you want to operate the organization's sphere of influence? If yes, then work is likely to be highly satisfying. If the answer is no, it is likely to be extremely frustrating. A biologist who wants to address national issues of conservation is likely to be unhappy working for an organization that deals only with local or regional concerns.
3. *Are the people I would be working with individuals I can respect and trust, and with whom I share common interests?* It is often uncertain, given limited contacts with potential co-workers, exactly how relationships will develop in an organizational environment. A measure of optimism is appropriate. Blind faith is not. If potential co-workers display obvious behaviors or attitudes you cannot accept, practice patterns of work and activity showing a lack integrity, or display a philosophy of work or management that you are opposed to, then decline the position. Never, in any circumstance, accept a position with individuals whom you know beforehand you do not like and respect, regardless of their professional prestige. Consideration of your personal "boss" will be even more important. It is a common saying among professionals in human resources that people don't leave jobs, they leave supervisors. It is a sad statement, but one so often verified by experience that it has become a proverb. Find out who your supervisor will be. Make a careful assessment of whether or not you can work with that individual.

TABLE 14.7. Contrasting constraints, rewards, and goals of conservation managers and academic researchers.

Job Component	Conservation Manager	Academic Researcher
Motivation	Questions driven by need to answer specific problems, eye toward application	Questions driven by theory and basic science
Goal(s)	Provide data to manager to guide management; derive guidelines for action	Publish in high-quality journals; compete for research funding
Service	Explicit responsibilities to agency; realistic goals	Work within context of publicly supported and idealistic goals
Time frame/work schedule	Work quickly to obtain data; long planning range of agency budget process	Conform to class schedules and academic calendar; projects chosen to fit thesis and dissertation schedules of graduate students
Staffing	Cost-effective workers	Train students in modern techniques; find students jobs; recruit and support new students
Financial considerations	Accomplish as much as cost-effectively possible	Support projects via grants; recover indirect costs for home institution

Source: Adapted from Huenneke (1995). Table format by M. J. Bigelow.

4. *Is my job something that I can do effectively and with satisfaction?* Even in the best organizations, jobs vary. Is the proposed job description one that offers an opportunity for you to display your strengths, grow in your competencies, and contribute to the organization's goals in ways meaningful to the organization and to you? An effective and satisfying position should provide a clearly defined organizational role, and should involve the individual in decision-making that is appropriate to that role and relevant to his or her expertise.

14.5.2. How Can I Excel?

In more menial jobs, tasks are specific, deterministic, and easily evaluated. Retention is based on meeting minimum standards of performance and productivity. In more meaningful work, such as a career in conservation biology, both the job and its evaluation are more fluid and require creativity and imagination. Meeting minimal expectations of written job descriptions is unlikely to lead to satisfaction or advancement, and may even result in dismissal. Effective workers follow certain principles in approaching their assigned tasks, and in making strategic decisions about which organizational tasks to take on when they have the freedom to choose tasks themselves.

1. *Make work output responsive to meeting the needs of others* – Every occupational task and output, whether written reports, oral presentations, management decisions, or data analyses interfaces with others in the organization who might use such output in their own tasks. Before undertaking a task, determine: (1) Who will receive the output? (2) What questions should this output answer to help to them accomplish their goals? (3) In what format should this output be presented so it can be adapted to other contexts? Employees who consistently produce output with their co-workers' needs in mind, and who frame their work in ways that make it easy for others to use and integrate their efforts in other ways, are employees who become more influential in organizational life and who are most appreciated and respected by others.
2. *Determine the indispensable needs of your organization or workgroup, and make yourself the person who meets these needs through your work output.* While all organizations manifest a diversity of work output, there are certain core objectives in work that must be accomplished or the organization will cease to function. Given a measure of freedom in tasks and priorities, an employee who gives priority to completing the organization's indispensable tasks soon becomes the organization's indispensable person. This is done by determining what the indispensable needs are, and then fulfilling these indispensable needs in a relentlessly consistent manner.

14.5.3. Nurturing Professional Relationships

Current research on organizational productivity reveals that the most effective and productive organizations are those that manage through relationships, or, as it is sometimes expressed, those that manage networks rather than tasks. Effective leadership does not attempt to control others but to inspire others to share common goals and take ownership of organizational tasks that will accomplish them. Such an approach requires a high quality of relationships in a work environment. Quality of relationships can be maintained by pursuing certain principles in relationships with fellow workers.

1. *Seek to build relationships in a work environment based on common goals, shared tasks, and shared credit for accomplishment.* To the extent possible, expand your own work tasks and objectives to include the work of others. When this strategy is followed, it not only produces better work with wider applications, it produces a work environment in which people share in the fruits of accomplished tasks.
2. *Take a genuine interest in the welfare of others and build trust by understanding their needs and being an active part of meeting them.* Organizational relationships without trust, no matter how efficiently designed, simply do not work. Trust is established by deliberately being attuned to both the professional and personal needs of fellow-workers and, whenever possible, being a resource that helps such needs to be met.
3. *Involve others in decision-making.* People do not support what they do not create. Every person who has a stake in creating an organizational objective has a stake in achieving it. Work at creating opportunities for others to share in decision-making processes, and especially in contexts where they can make constructive contributions.

14.6. Becoming an Effective Advocate for Conservation

14.6.1. Professional Expressions of Advocacy

The relationship between science and advocacy has traditionally been one of strict separation, in order to avoid any contamination of professional objectivity. But conservation biology is not a traditional science, and anyone who pursues the practice of conservation biology as a vocation will invariably be brought into contact with issues of conservation advocacy. Remember that historically conservation biology began as an advocacy movement in science (Chapter 1). In its early years, members of the Society for Conservation Biology were, for all their professional struggles, relatively unified in the view that conservation biologists must speak and stand against the threats to biodiversity, and work against the extinction of species, not only in scientific studies, but in their appeals to managers, policy makers, and the public at large. They unapolegetically saw themselves as advocates for biodiversity conservation. As conservation biology has grown more respected and established, complete with its own departments, graduate programs, endowed chairs, journals, and funding sources, a more traditional and conservative approach to advocacy has, perhaps predictably, set in. As a result, the controversy over the proper role and engagement of scientists in postures of advocacy for conservation has not disappeared. It has continued and intensified. The issues of advocacy are complex, and must be considered carefully and reflectively by everyone who aspires to vocation as a conservation biologist.

Some conservation biologists, like Peter Brussard and others have argued that activism by conservation biologists should occur "outside of our professional society" and that conservation biologists and conservation activists should, as groups, maintain "a strategic and measurable distance" from one another (Brussard et al. 1994). This stance is consistent with the view that conservation biology is a form of regulatory science (Chapter 3) that should be understood as "the application of classical scientific methodology to the conservation of biological diversity" (Murphy 1990:203). Conservation biologists with this perspective argue that "Conservation biology exists only because biological information is needed to guide policy decision-making." Therefore "the practice of conservation biology ends where science ends and where advocacy begins" (Murphy 1990:203). If this is a correct perspective, then conservation advocacy, specifically the act of working toward a normative outcome or condition in conservation management or policy, is not conservation biology. Rather, the role of conservation biology is to provide scientific knowledge to resolve technical questions associated with the formation of conservation policy. But this is not the only view.

14.6.2. An Alternative View of Advocacy

Conservation biologist Graeme Caughley asserted that "the saving of a species from extinction has always been a paramount responsibility within the field of biology" (Caughley 1994). But to assert that science has a "responsibility" to save species is a normative, value-laden statement of advocacy that makes no sense unless one appeals to a standard of what "ought" to be the correct application of scientific knowledge. The birth of conservation biology is rooted in such normative assumptions that formed the basis of its identify and mission (Chapter 1), and the rapid growth of conservation biology has been a testament to their appeal. In attempting to define the discipline in its early years, Michael Soulé wrote, "conservation biology is a crisis discipline grounded in the recognition that humans are causing the death of life – the extinction of species and the disruption of evolution" and that conservation biology is a response by "those scientists who feel compelled to devote themselves to the rescue effort" (Soulé 1991).

The proposition that the sole job of conservation biologists is to provide information to managers and policy makers could be called *conservation positivism*, or perhaps the "just study it" approach to conservation problems. This view is problematic on three counts. First, conservation biologists must make *a priori* decisions about what information to present and how to present it. This is not a question of unscrupulous manipulation but of legitimate scientific perspective, and such perspective is determined, in part, by what the biologist understands to be the normative uses and values of the information. Second, managers and policy makers often interpret objective information, such as model results, as offering normative diagnoses and prescriptions (such as why a population is declining and what to do about it) instead of seeing model results as objective descriptions of "what would happen if" certain conditions prevail. Clouded by this misconception, policy makers often present normative recommendations to the public as if such recommendations were objective and inescapable conclusions dictated by the model, not by their own normative values. For example, managers and policy makers often use ecological and population models to legitimize policy decisions rather than inform the public (or, in some cases, themselves,) about the consequences of possible decisions they could make. In the words of environmental modeler J. B. Robinson, "By cloaking a policy decision in the ostensibly neutral aura of scientific forecasting, policy makers can deflect attention from the normative nature of that decision …" (Robinson 1992). As noted earlier (Chapter 2), management decisions are inherently value laden, and conservation managers are constantly engaged in a process of trying to both understand and value ecological processes, precisely because they must choose the point at which they intervene in such processes. They must then communicate the reasons for their intervention to diverse public interests. Therefore, conservation biologists should ask themselves if they would be better off to consider and evaluate normative values in their presentation of data and recommendations or to let managers and policy makers use their results to make policy decisions that are disguised as value-neutral statements allegedly dictated by model results or other kinds of scientific facts. And if that is the case, would it not be appropriate to be an advocate of the "better" management plan than the "worse" one?

This second problem leads to a third. If conservation biologists do not consider normative values associated with their research, they may find themselves addressing trivial questions instead of issues of significance. For example, Graeme Caughley (1994) asserted that a primary query answered by population viability analysis – how long a population will persist – is a trivial question. Having a specific answer does not make the question any more significant. The significant questions, according to Caughley, are, what is putting the population's persistence in jeopardy, and what can we do about it? But to answer the latter question implies a value judgment, that the population *ought to persist*, and its solution requires not merely provision of information but changes in human behavior, as well as specific social and political outcomes that change conditions causing endangerment. Working towards these ends sounds suspiciously like advocacy.

If conservation biology must be defined as information driven, then its research is to be dedicated to needs defined by management and policy and to the consequences of management decisions. It need seek no particular outcomes. Further, it need not be overly concerned with interdisciplinary study because specialization will remain the most productive and efficient path to generate the greatest quantity and precision of information. On the other hand, if conservation biology is value driven and mission oriented, it must not only pursue research defined by management need and by the consequences of management decisions, but it also must engage the process of management itself, offering *recommendation* as well as *information*. In the latter case, interdisciplinary approaches become essential, because conservation biologists would now really need to speak conversantly with the public and with other disciplines, to consider and take responsibility for societal outcomes, and to rigorously evaluate an array of such outcomes against different, sometimes conflicting, standards.

14.6.3. Examining Outcomes: Implications of Alternative Views of Advocacy

One's perspective on this question will determine their view of advocacy in conservation. The most conservative view is sometimes called ***professional advocacy*** or, more colorfully, the "trickle down" theory. Again to quote Brussard, and, in this case, his colleague John Tull, "Professional advocacy involves informing policy makers, managers, and the public about issues that arise in one's area of expertise" (Brussard and Tull 2007:210). According to this view, publication in books and journals is the only appropriate outlet for information transfer. This kind of advocacy is occasionally effective, but it is always slow. Even Brussard and Tull admit that, in their own work, this kind of advocacy is too slow to do any good. Recall Beever et al.'s (2003) study of pika extinctions and their pattern corresponding to predictions of climate change (Chapter 5). Brussard, one of the principal investigators in that study, and Tull admit that, in this case, "Because of the importance of these findings, we distributed reprints of this article to agency heads at a Nevada Biodiversity Initiative meeting. By speeding up information transfer in this way the Nevada Department of Wildlife incorporated the findings from this paper into their Comprehensive Wildlife Conservation plan for the state in 2005" (Brussard and Tull 2007:21). Well now, isn't the assertion that these findings are "important," and not merely "interesting" suggest a judgment about the value of pikas? And doesn't this pattern of behavior, namely handing out reprints of the pika study directly to the decision makers at the decision-making meeting look at lot more like direct advocacy for pikas than like the strict spirit of "professional advocacy" that only transfers information through books and journals?

Brussard and Tull commend other forms of advocacy for conservation biologists if it takes the form of: (1) advocacy for science (presenting a positive view of science as a method and way of knowing about things, including conservation issues, to the general public); (2) advocacy for ecosystem services (speaking as an advocate for the economic and material value of goods and services provided by ecosystems and ecosystem processes); and (3) advocacy for the natural world (speaking as a advocate for preserving undisturbed nature and encouraging human experiences in it) (Brussard and Tull 2007). One can hardly argue with these forms and subjects of advocacy as appropriate for conservation biologists. One can hardly find any inspiration or usefulness in them either. Endangered species and ecosystems will not be saved by extolling platitudes about the value of "the natural world" when the threat to individual species and habitats is particular, direct, and obvious. If *particular* species, habitats, and ecosystems are to be preserved, what kind of advocacy will get this done, and can a conservation biologist engage in it?

Carol Brewer expressed the problem of traditional professional advocacy this way. "We do not have time," wrote Brewer, "to wait for our discoveries to "trickle-down" to the public through the filters of textbooks and other media. We must take more responsibility for translating the results and significance of our research in a way the public – our families, neighbors, and communities – can understand" (Brewer 2001:1203). Brussard and Tull apparently did not think that pikas in Nevada had time for the "trickle-down" method either. In fact, Brewer's use of the phrase "we do not have time" indicates an assumption of urgency driven by a moral imperative: we *must* save these species! Let the imperative be granted. If so, what is the best kind of advocacy to express and advance it?

The "trickle-down" method is ineffective, and it is now being criticized with increasing severity on a global scale. Erik Meijaard of The Nature Conservancy in the province of East Kalimantan, Indonesia, and his colleague, Douglas Sheil of Indonesia's Center for International Forestry Research, took on the problem of the "trickle down" advocacy approach in their provocative paper, "Is Wildlife Research Useful for Wildlife Conservation in the Tropics?" (Meijaard and Sheil 2007). After examining 284 recent publications on tropical wildlife studies, including 153 from peer-reviewed journals, Meijaard and Sheil concluded that few of these studies "… address threats to species and fewer still provide input for or guidance to effective management.… Research is seldom judged on its relevance to pragmatic problem solving. Furthermore, many research programs lack the necessary long-term vision and organizational structure for useful applied research. We consulted conservation leaders about our conclusions and all responses suggest that our concerns are not unique to Borneo but reflect wider problems. We conclude that conservation research across most of the tropics is failing to address conservation needs" (Meijaard and Sheil 2007:3053). If Meijaard and Sheil are right, conservation requires an approach to advocacy made of sterner stuff than the traditional "professional advocacy" described by Brussard and Tull, even if one does hand out the right reprints at the managers' meeting. What would such advocacy look like?

Recall from Chapter 1 Daniel Rohlf's description of conservation biologists as ***focused advocates*** (Rohlf 1995a). Rohlf defined a focused advocate as a person or group reporting data concerning an area in which he or she has expertise as well as deeply held convictions, and who works to ensure that the information presented is correctly interpreted and rightly applied. Many conservation biologists believe that focused advocacy, including the development of regulations and policies to conserve biodiversity, is an inherent responsibility of being a conservation biologist (Noss 1989; Thomas and Salwasser 1989; Dudley 1995; Rohlf 1995b). Focused advocacy provides specificity that avoids vacuous platitudes like supporting "advocacy for the natural world" because it speaks to particular needs of particular species, places, and processes. But if there are legitimate forms of advocacy to pursue, are there forms of advocacy to avoid?

14.6.4. Avoiding Conflicts of Interest in Advocacy

Suppose you are a conservation biologist who works for a private environmental consulting agency in the United States. As shortages of oil make natural gas a more attractive fuel option for some forms of energy use, an energy company is motivated to search for prospective natural gas supplies on large private ranches in a remote area in a western state. The ranch lands are heavily used by wildlife, one of the most visible and attractive being elk. Drilling to find and remove the natural gas destroys vegetation on the drill site, but the energy company has various options on each drill site to attempt revegetation and reclamation. The energy company asks your firm to conduct an experimental study of the various restoration methods and report how elk respond to each of them. Specifically, they want to know, if the elk used drilled areas before disturbance, do they return to the site after drilling is over or not? If so, are their use rates the same or different than they were before drilling? Does the operation cause a permanent loss or degradation of habitat, or a long-term change in a site's biodiversity? Which reclamation techniques best preserve or enhance natural biodiversity and natural levels of elk use of the site? Your employer takes on the project, with a contractual understanding that the energy company will pay your firm for the service of its investigation regardless of the findings, and will in no way attempt to influence the findings of the study or their interpretation. With that commitment in the contract, your firm agrees to prepare and present the results of its investigation in a final report to the company at a specified time.

This kind of scenario is not uncommon, and the arrangement depicted is perfectly ethical under the constraints described. In this case, the consulting firm takes the role of an information provider, and neither the firm nor the energy company, its "client," takes on the role of an advocate. But just to make things more interesting, suppose that a group of local citizens becomes concerned about the drilling activity, not only because of potential detrimental effects on elk and other wildlife and their habitat, but because of the potentially negative effects on the aesthetics of the landscape, and the potential for negatively affecting local economies and culture by creating a sudden "gas boom" in an area that has historically been dominated by an agricultural economy. They form an organization whose mission is to stop natural gas exploration in the local area.

As a biologist who lives in and enjoys the area, you are sympathetic to the aims of the the local citizens' organization. But should you join the organization and be an advocate for its mission while this study is in progress? Here the answer would be "no." Taking a position against drilling for natural gas while at the same time conducting a study to determine the *effects* of such drilling on wildlife and habitat conditions would create a conflict of interest. Your interest in professional scientific objectivity (what really happens on a drilling site after drilling is over) is in conflict with your interest in stopping the drilling altogether, which would be your stated aim as a member of the protective organization. In this case, the right thing to do is to NOT join the protective organization, but to continue your research and present the outcomes of it in a fair and professional manner. Now there is only one interest (scientific professionalism and the pursuit of truth) and that interest is not in conflict with itself. It is for this reason that many private conservation organizations, consulting firms, and government agencies prohibit, as part of their employee contract agreements, membership in other conservation organizations whose specific missions might create a conflict of interest with their mission. Thus, when you consider employment with any kind of conservation organization or entity, consider the implications of that employment on your own role and activities as a conservation advocate, and whether you can accept those implications and limitations that come with the job and the agency you work for.

Advocacy is an integral part of conservation biology, and your own views on and level of interest in advocacy should be built into your own personal mission statement. Such views should be one of your most important criteria to consider as you explore different kinds of conservation vocations and employment. Some kinds of work in conservation biology are almost entirely about advocacy. Other types of conservation efforts require that work and advocacy be kept separate from one another, and many kinds of work in conservation biology fall somewhere in between. Specifically, you should ask, "Am I pursuing a career in conservation biology in order that I might provide information about the biology of endangered species or in order that I might provide expertise in how to save endangered species? Do I wish to focus on the measurement of biodiversity, or to provide an informed analysis of how to preserve it?" Perhaps the most important question is, "Do I wish to work with an institution or community that provides information about how to conserve species, or do I wish to be a member of an organization that actively uses such information for species preservation?"

An individual doing work in one category is not more or less of a conservationist than someone working in a another category. But if that person is you, it is your responsibility to be happy, and free from internal conflict, in the professional life you have chosen. Therefore, the issue of advocacy is one you must address in advance, before the choice of employment is made, so that you will not have to make hurried and, perhaps, rash responses to issues of advocacy in the heat of crises or conflicts that will inevitably occur in the work, including your work, of conservation.

14.7. Synthesis

This chapter has taken the risk of offering some prescriptive advice because conservation is performed by conservationists, not by words in a textbook that magically assemble themselves into correct conservation actions. I encourage all students of conservation biology to consider what the future may hold for themselves and their discipline. We make the future every day by every daily choice. Our choices reflect our commitments to what we truly value. There are three key principles to success in pursuing an effective education and vocation in conservation biology. The first is the principle of personal responsibility. You, not your college, advisor, roommate, parents, income level, national origin, or upbringing are responsible for the outcomes of your education and your vocation. You cannot always control the circumstances and stimuli thrown at you in the great adventure of life, but you will always have the freedom to choose how you will respond to them, if you remember to use that freedom. We are not determined by what others do for us or to us, although we may be helped or hurt by their actions. Rather our identity and character as human beings are determined by how we choose to respond. This is the essence of human freedom, the freedom of self-determination, no matter what the limitations of circumstances. The second principle is to define what you value. There is no satisfaction in climbing the ladder of success only to find it was leaning against the wrong wall. Be sure of what you value and pursue that. The third principle is: take action. If you accept personal responsibility for how you are going to respond to the circumstances and opportunities of your life, and your career in conservation biology, and if you know what you value achieving in this career, then take concrete action in a pre-considered plan to pursue that goal.

It has been noted by past conservation biologists that conservation problems often start out as biological problems but eventually turn into people problems (Teague 1979). Conservation biologists Susan Jacobson and Malory McDuff put the matter more plainly. "In reality, people are in the beginning, middle, and end of all management issues. Recognition of this central role will improve our ability to conserve nature. Conservation is a human endeavor driven by people's values toward the management of land and resources. Preservation of biodiversity depends upon public commitment to its protection" (Jacobson and McDuff 1998:263). In the end, the most basic and fundamental goals of conservation biology, the preservation of Earth's biodiversity in its living systems, with their health and integrity, will not be ultimately achieved by improvements in technology, economics, or information transfer. An Earth in which the world's biodiversity fully lives will be one in which there is a different kind of human being present, and a different kind of human community, one that understands and is committed to the value of non-human life and to all the things needed to sustain it. Only those conservation biologists who become these sorts of people, and who can influence others to do the same, will make a contribution toward this ultimate goal. Consider this text an invitation to join this effort, and to make your own work a living part of it.

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Glossary

A

acidification
The process through which the pH of surface fresh waters, especially lakes, declines because of inputs of acidic precipitation in the form of rain, snow, or fog.

adaptive management
The structuring of policy or management actions as a set of testable hypotheses to promote learning from policy implementation, and the subsequent design and use of management actions as ongoing experiments intended to provide reliable information about the system and inform future management decisions.

age structure
The proportion of individuals in a population at each age, or in each age category.

Allee effect
The decrease in population growth rate in a small population, occurring when individuals do not often encounter potential mates.

allelic diversity
The average number of alleles per genetic locus.

allozymes
Different allelic variants found at a single gene locus. Allozymes bear electrical charges, which differ among allozymes as a reflection of differences in their enzyme proteins.

allozyme electrophoresis
A molecular technique to assay genetic variation by separating enzyme proteins through their movement in a chemical medium (gel) to oppositely charged poles in an electric field.

alpha diversity
The diversity of species within a community (i.e., species richness) on a specific site.

alpha rarity
Rarity or reduction in numbers of individuals of each species on a site or in a community that occurs as more species are added to the site or community; i.e., rarity in numbers of individuals of a species in a site-specific population that occurs as the site increases in species diversity.

alternative stable states
In lake systems, the potential for different conditions to prevail at similar nutrient levels, with rapid transitions occurring between states (e.g., from abundant submerged macrophytes in clear water, to dense phytoplankton in turbid water).

aquatic ecological system
Stream networks representing a range of areas with distinct geomorphological patterns connected by similar environmental processes such as hydrologic, nutrient, and temperature regimes.

aquatic zoogeographic unit (AZU)
The highest level of classification in a coarse-filter classification system for streams, lakes, and rivers which also serves as the overall planning unit in initial conservation assessment. AZUs conform to major freshwater drainage boundaries, generally 10,000–100,000 km^2 and are distinguished by differences in continental and regional zoogeography.

areteology
A system of ethics that gives primacy to the formation of virtue, the capacity to act with moral excellence in every circumstance.

average heterozygosity
The average proportion of individuals in a population that are heterozygous (carrying two different alleles) for a particular trait. This metric reflects the proportion of heterozygous individuals measured across several loci. As a metric, average heterozygosity is used as a measure of genetic diversity in a population.

B

basic rule of conservation genetics
The assertion that natural selection for performance and fertility can balance inbreeding depression if the change in

the inbreeding coefficient (ΔF) is no more than 1% per generation. The 1% rule is referred to as the *basic rule of conservation genetics* because it serves as the basis for calculating the irreducible minimum population size consistent with the short-term preservation of fitness.

bequest value
The value of knowing that something is preserved for future generations.

beta diversity
A measure of the rate of change in species composition of communities across a landscape.

beta rarity
Rarity that occurs in species that are habitat specialists which are abundant in one (optimal) environment, but rare or absent from environments which manifest even slight changes in one or more critical variables, and therefore show a pattern of overall rarity across a landscape.

binomial nomenclature
A system of naming species devised by Swedish botanist Carol Linn which assigns a unique, two-word Latin name to every species, and thus permits scientists from any part of the world to have a common standard of nomenclature when speaking of individual species. The second word in the binomial is the creature's species name, which signifies traits unique to its own kind. The first word is its genus name, a larger or "higher" taxonomic category in which it might be placed with other creatures like itself, yet different.

bioclimate envelope
Models that define the climatic tolerances of a species by discriminating between the climates of locations inside and outside the species range based on particular climate variables, such as minimum and maximum temperature.

biodiversity
The entire array of earth's biological variety, contained in genes, populations, communities, and ecosystems.

biological species concept
The idea that species are defined by reproductive isolation. By this definition, species are organisms that breed together to produce viable offspring resembling the parents, but do not breed and reproduce viable offspring with other species.

biopiracy
The illegal acquisition of non-human biological material.

bioprospectors
Human agents who go in search of non-human biological material.

biotemperature
In the Holdridge Life Zone classification system, the mean value of daily temperature above 0°C divided by 365, which provides a measure of the heat available during the growing season.

blast fishing
The harvesting of fish through the use of explosives. Blast fishing, when employed near corals, leads to destruction of coral reefs.

bleaching – *See* coral bleaching

bycatch
Non-targeted species captured or killed in commercial fishing activities.

C

carbon sequestration
A method of reducing greenhouse gases by injecting CO_2 produced in other kinds of industrial processes into deep underground wells or beds of underground minerals so that it does not enter the atmosphere.

Certified Emission Reduction Units (CERU) – *See* Clean Development Mechanism

cladistic approach
A taxonomic approach which views a group of similar species as a lineage of ancestral-descendent populations (clade). Different species in a clade are distinguished from one another by the relative proportion of shared primitive and derived features.

Clean Development Mechanism (CDM)
A procedure for allowing an investor in an industrialized country, whether industry or government, to invest in an eligible carbon mitigation project in a developing country and then be credited with Certified Emission Reduction Units (CERU) that can be used by the investors to meet their own obligations to reduce greenhouse gas emissions under the Kyoto Protocol.

Climate Change-Integrated Conservation Strategies (CCCS)
A procedure in which bioclimate envelope models are used to develop conservation strategies to mitigate effects of climate change using global climate models, regional climate models, dynamic and equilibrium vegetation models, land-use models, site-specific sensitivity analysis and other analytical approaches and techniques.

climate niche
The sum of a species' tolerance ranges of climate variables.

coercive measures
In the context of international law, sanctions, penalties, loss of membership in international organizations or of privileges in international dealings which are used to motivate unwilling parties to comply with legal standards, such as international environmental agreements.

co-management
A conservation strategy that attempts to simultaneously address biological, cultural, economic, and political concerns through collaboration and integration of conservation efforts between local communities and government authorities.

common pool goods
Goods where one user's consumption subtracts from the supply available for others, yet the physical nature of the resource makes it difficult to exclude users.

community-based ecotourism (CBET)
Travel to and recreation in natural environments by non-resident individuals (tourists) for the purpose of enjoying the biodiversity or ecosystem characteristics of such environments, but practiced in such a way that it conserves the environment and sustains the well being of local people.

compartmental model
A model that organizes and displays explicit, usually quantitative, information about the state of, connections between and relationships among specific and discrete components of a population, landscape, or ecosystem.

compliance
In the context of international law, the extent to which the behavior of a state, as a party to an international treaty, actually conforms to the conditions of the treaty.

compliance information systems
In the context of international law, systems whose aim is to ensure compliance and report non-compliance.

conceptual model
A visual or narrative summary that describes or identifies important components of a system and the possible interactions among them.

connectedness
The presence of physical linkages between landscape elements.

connectivity – ***See also*** **habitat connectivity**
A parameter of landscape function that measures the processes by which subpopulations of organisms are interconnected into a functional demographic unit, achieved only if organisms actually move between connected units.

connectors
In a model, elements that explicate or display the path through which material or individuals are transferred from one stock to another or from sources to sinks. *See also* Source, Stock, and Sink.

conservation easement – ***See also*** **zoning**
A special case of land use zoning, applied specifically to conservation and developed to make the value of conservation on private land more explicit and profitable to landowners. In an easement, the landowner agrees to restrict some activities or forms of development on his or her land to achieve specific conservation goals. Such restrictions lower the assessed value of the land, generating a reduction in property taxes for the owner and a reduction in inheritance taxes for the owner's heirs.

conservation management unit (MU)
A population or group of populations that show evidence of genetic relatedness, but also are arranged spatially in such a way that they can benefit from a common management strategy.

contingent valuation (CV)
The assignment of economic values to nonmarket goods through analytical methods that determine an individual's willingness to pay for such goods or willingness to accept compensation for their loss.

converters – ***See also*** **parameters**
Values of variables that determine rates of flow or movement of resources or individuals from one state to another or from one area to another.

coral bleaching
A phenomenon that occurs in corals exposed to extended periods of elevated water temperatures resulting in the loss of the cells and pigments of symbiotic dinoflagellates (zooxanthellae) that live within the coral.

corridor
A linear pathway that connects habitat patches and allows organisms to move among them.

critical habitat
As defined by the US Endangered Species Act, habitat of special significance to the survival of an endangered or threatened species

critical threshold – ***See*** **percolation threshold**

D

data mining
The systematic search and interpretation of past records to inform present conservation management decisions or policies.

deadweight social losses
Distortions in economic efficiency and market function caused by the diversion of earned income to the government through taxes.

decision analysis
A management approach that attempts to determine the probability of different population events, such as persistence or extinction, that would result from specific management decisions, actions or strategies.

declining-population paradigm
A body of concepts focusing on the understanding the deterministic processes responsible for population decline and how to mitigate or reverse threats to population persistence.

demersal species
In aquatic environments, bottom-dwelling species or "groundfish" such as flounder and haddock.

demographic stochasticity
Random fluctuations in birth and death rates, emigration and immigration, or sex ratio and age structure of a population.

deontology
A system of ethics that gives primacy to the fulfillment of obligations and duties.

deterministic factors
Factors that affect a population in a constant relation to the population's size.

diffusion coefficient
A value equal to one-half the mean squared distance moved in a time unit by an organism.

direct payment (DP)
In conservation, payment to individuals or local communities for protecting or restoring ecosystem services which benefit others.

dispersal
The act of leaving an area of birth or present activity to move to another area.

dominance-diversity curve
A curve that depicts the relationship between the relative species abundance in a community and species rank in abundance in the same community. The relationship is usually inverse (species rank in abundance declines are relative species abundance increases) and becomes steeper as the number of species declines, such that, in communities with few species, common species become extremely dominant numerically.

E

ecocentrism
An ethical position asserting that the value of land and its component plants and animals is derived from their contributions to the function and integrity of the ecosystem and its processes; therefore the highest good is to preserve the functional integrity of the ecosystem.

ecological drainage unit (EDU)
Regional biodiversity distinctions within aquatic zoogeographic units (AZUs), generally 1,000–10,000 km^2 in size, which are delineated and classified by identifying areas with similar biotic patterns.

ecological economics
A school of economic theory designed to achieve a union of economics and ecology such that the economy is conceived as a subset of the global ecosystem sustained by the flow of energy and material from and back to that ecosystem.

ecological redundancy
A measure of the number of species or groups involved in rate-limiting ecological processes in a given ecosystem, i.e., an estimate of how many species or groups perform the same or similar ecological functions within the same system.

ecological succession
A pattern of continuous, directional, nonseasonal change of plant populations on a site over time.

ecosystem
A biotic community interacting with its physical environment.

ecosystem management
A pattern of prescribed, goal-oriented environmental manipulation that (1) treats a specified ecological system as the fundamental unit to be managed; (2) has a desired outcome of assuring the persistence of historical components, structure, function, products, and services of the system within biological and historical ranges and rates of change over long time periods; (3) uses naturally occurring, landscape-scale processes as the primary means of achieving management objectives; and (4) determines management objectives through cooperative and deliberative decision-making by individuals and groups who reside in, administer, or have vested interests in the state of the ecosystem.

ecotourism – *See also* community-based ecotourism (CBET)
Travel to and recreation in natural environments by non-resident individuals (tourists) for the purpose of enjoying the biodiversity or ecosystem characteristics of such environments.

edge
The boundary between different types of habitat at which there occurs an exchange or flow of energy, material, and/or organisms along with alterations in biophysical processes and ecosystem composition and structure.

edge effects
A suite of processes and factors associated with edge environments, which become more pronounced when habitat is fragmented and the relative amount of interior (non-edge) habitat decreases.

edge influences – *See* edge effects

effective population size
The size of an "ideal" (randomly mating) population that would undergo the same amount of genetic drift as a particular real population.

effectiveness
In the context of international law, the degree to which the fulfillment of the conditions of a given law, treaty or convention actually achieves the objectives of the law, treaty or convention.

Ehrlich Identity
An expression of the relationship between human population, human resource consumption, and human technology and environmental impact, formally expressed as

$$I = P \times A \times T;$$

where I is environmental impact, P is population, A is affluence (a measure of consumption), and T is technology (an index of efficiency of resource use and pollution abatement). The Ehrlich Identity asserts that environmental impact is a function of the combined effects of human population density, per capita consumption (A) and efficiency of resource use (T).

elasticity
A type of sensitivity analysis that determines the effect of a variable on model outcomes; the degree to which a change in the value of a model variable changes the value of λ, the population's rate of growth, in relation to other model variables.

endemism
The condition of restriction of a species to a particular area or region.

enforcement
In the context of international law, actions used to force states to first implement and then comply with international laws and agreements.

environmental insurance bonding
The practice of requiring an individual or company about to engage in potentially harmful environmental activities to post, in advance, a bond equal in value to the cost of repairing harm that could result from such activity, should it occur.

Environmental Kuznets Curves (EKC)
A family of graphical representations of the relationship between environmental deterioration and per capita income for various environmental variables. A typical Kuznets Curve shows increasing environmental deterioration with increasing income to an "inflection point" or "turning point income," past which further increases in income are associated with declining levels of environmental deterioration.

environmental stochasticity
Fluctuations in the probability of birth and death in a population because of temporal variation in habitat parameters, climatic variation, competitors, parasites, predators, diseases or other environmental factors external to the population.

environmentally sustainable
A practice, process, or product that can be used at the same rate over time without loss or diminishment of its quality, productivity, or other capacities.

epistasis
The interference with or suppression of the effect of a gene by a different gene, often manifested in the interactive effects of co-adapted genes.

ethics
Systematic organizations of values that establish principles for conduct and behavior.

eutrophication
The process in which the release of nutrients, particularly phosphorus, into streams, lakes, or estuaries triggers a chain of events resulting in oxygen depletion, turbidity, and radical alteration of the biological community.

evolutionary species concept – *See also* phylogenetic species concept
The idea that a species is one lineage evolving separately from other lineages.

excludable goods
Goods or resources in which ownership permits the owner exclusive use of the goods or resources and provides the owner with the ability to exclude others from such use.

existence value
The value of knowing that something exists.

exponential population growth
A model in which population size increases at an ever-increasing rate, and only the population's size (N) and intrinsic rate of increase (r) determine the change in numbers of individuals.

F

FBO
A faith-based organization engaged in conservation that uses and applies religious principles and teaching to solve conservation problems, formulate management decisions, or determine long-term conservation strategies.

factor resolution
A population monitoring tool in which experiments are conducted to determine which factors actively limit population growth.

fecundity
The number of gametes produced per female per unit time.

fixation of deleterious alleles
A condition in which all individuals in a population possess only the harmful allele among multiple alleles at a particular locus, such that the trait or traits associated with the allele become permanent or "fixed" in the population. The risk of such fixation increases with decreasing population size.

flexible assurance bonding – *See* environmental insurance bonding

focused advocate
A person or group reporting data concerning an area in which he, she or they have expertise as well as deeply held convictions, and who works to ensure that the information presented is correctly interpreted and rightly applied.

function-based indicator species
Species that determine the characteristics of the ecosystem in which they live because of ecological functions they perform in the system.

functional analogs
Species that play the same ecological role in a community (members of the same functional type).

functional types
Species groups that fill various and different ecological roles in a community, also called "guilds" among animals and "life forms" among plants.

fund-service resources – *See also* stock-flow resources
Resources that are not materially transformed into what they produce, which can only be used a given rate, and

whose production is measured as an output per unit time (rate) and therefore cannot be stockpiled. The maintenance of water quality by an intact forest is an example of a fund-service resource.

G

GAP analysis

Originally an acronym for Gap Analysis Program (GAP), a type of analysis that determines, through the use of computer overlay maps and other forms of spatial analyses, whether populations of species targeted for conservation fall within the boundaries of currently protected areas and which elements of landscape biodiversity are underrepresented in reserve systems. The final outcome of a GAP analysis is to attempt to identify the "gaps" in the conservation reserve network: where in the landscape have significant biodiversity resources been left unprotected?

GIS

An acronym for Geographic Information System, a computer-assisted system of spatial analysis designed for the acquisition, storage, manipulation, analysis, and display of geographic data.

GONGO

A Governmental and Non-Governmental Organization (GONGO), such as the World Conservation Union (IUCN), whose members and contributors are nations and organizations, rather than individuals.

gamma diversity

The rate of change of species composition with respect to distance in a landscape, particularly at regional scales or larger.

gamma rarity

Species that may have large populations in local communities and demonstrate broad environmental tolerances, but are restricted to particular geographic areas and so become increasing rare with increasing distance from their population centers.

Gause's Law of Competitive Exclusion

The rule that different species are able to live together in communities only if they differ sufficiently in niche separation, that is, in the way they use resources. Put negatively, the assertion that two species cannot coexist in the same community at the same time if they occupy the same ecological niche.

gel electrophoresis – *See* allozyme electrophoresis

Gene Conservation Reserve (GCR)

A conservation reserve which has been established to preserve the genetic diversity of targeted species or other taxonomic groups.

Gene Diversity

The probability that two alleles from the same locus sampled at random from the population will not be identical by descent. Mathematically, Gene Diversity (*GD*) is equal to

$$GD = 1 - MK$$

where *MK* is population mean kinship.

gene flow

The effective movement of genes between populations or population subdivisions, which can be mathematically determined, in one way, from the expression

$$N_e m = \frac{1 - F_{ST}}{4F_{ST}},$$

where N_e is the effective population size, *m* is the rate of immigration and F_{ST} is the total genetic diversity found among all populations. The result is expressed in immigrants per generation.

Gene Resource Management Unit (GRMU) – *See* gene conservation reserve (GCR)

genetic drift

Random fluctuations in gene frequencies that occur as a result of nonrepresentative combinations of gametes during mating, especially in small populations.

genetic species concept – *See* also phylogenetic species concept

The separation of species according to genetic differences, such as restriction fragment length polymorphisms and amino acid sequence similarity.

genetic stochasticity

Fluctuations in demographic parameters, especially of small populations, through increased rates of inbreeding, genetic drift, and accumulation of unfavorable mutations.

genetically modified organism (GMO) – *See also* living modified organism (LMO)

An organism whose genome has been engineered or "spliced" so as to incorporate genes from other, usually very different, kinds of organisms in order to preserve, enhance, or add traits favorable to increased production, fertility, survivorship, or adaptability to particular environmental conditions.

geographic-based approaches

Approaches to biodiversity conservation that focus on the qualities of habitat and landscape that sustain resident populations rather than on the dynamics of individual populations.

gradient models

Models of habitat distribution in which different habitats are not clearly defined and environmental conditions change slowly and gradually at fine spatial scales.

greenhouse gases

Atmospheric gases, notably water vapor (H_2O), methane (CH_4), ozone (O_3), nitrous oxide (N_2O) and carbon dioxide (CO_2), that, because of their capacities to absorb infrared radiation radiated from the surface of the Earth, create a net influx of energy to the Earth and its atmosphere.

H

habitat

The place, or type of place, in which a species can persist.

habitat connectivity – *See also* connectivity

The degree to which individuals in a population can move between spatially disjunct patches of the same kind of habitat in a landscape, such that individuals in different patches function as a single demongraphic unit (population).

habitat conservation plan (HCP)

Under the US Endangered Species Act, an agreement between a federal agency (usually the US Fish and Wildlife Service) and a private landowner or non-federal government land owner that stipulates actions that will be taken by the landowner to enhance the population or habitat of an endangered species in return for permitting some mortality of the species on the property in the course of other activities carried out by the land owner (incidental take).

habitat edge – *See* Edge

habitat fragmentation

The breaking up of contiguous blocks of similar habitat or the disruption of patterns or processes associated with habitats, including subdivision of large blocks of habitat into smaller, isolated blocks.

habitat generalists

Species that can exploit a variety of habitats in a given geographic range and, thus, are relatively invulnerable to extinction through habitat loss or land-use changes.

habitat heterogeneity

Differences in habitats, at a variety of spatial scales, which may be natural (due to a rich internal structure of differing habitat patches) or artificial (due to fragmented habitats resulting from human activity).

habitat isolation

The separation of blocks of habitat from other blocks of similar habitat, a result of fragmentation.

habitat loss

Destruction, by human activities, of habitat for a particular species.

habitat specialists

Species that are typically highly successful in only one or a few types of habitat and, thus, are vulnerable to extinction through loss of their preferred habitat.

haplotypes

Mitochondrial DNA (mtDNA) groups that can be used to determine rates of gene flow among populations.

hard law

In the context of international law, formal conventions and treaties adopted by many nations, with explicit mechanisms for enforcement.

harvest refugia – *See also* no take zones

Areas, usually in marine environments, designed to protect a particular commercial stock or group of stocks from over-exploitation.

hedonic property model

A model of property value that treats such value as a function (f) of its structural characteristics (S), neighborhood (N), and environmental quality (Q), expressed in the identity

$$P_i = f(S_i, N_i, Q_i),$$

where the subscript i refers to each value for an individual (ith) property.

heterozygosity – *See also* average heterozygosity

In the context of genetics, the condition of or degree to which individuals in a population carry two different alleles of a gene for a particular trait, one from each parent, at the corresponding loci of a pair of chromosomes.

heuristic value

In the context of modeling and model building, the value associated with the indirect discovery of insights about the system, previously unsuspected interactions, or unforeseen characteristics of a population's demography or a system's environment that occurs in the course of building and using a model of the population or system.

homozygosity

In the context of genetics, the condition of or degree to which individuals in a population carry two identical alleles of a gene for a particular trait at the corresponding loci of a pair of chromosomes.

hotspot

A relatively small area with a disproportionately high level of biodiversity in multiple taxons.

hybrid

An individual produced by the mating of individuals of different species.

hybridization

Mating between individuals of different species.

I

implementation

In the context of international law, specific actions taken to make international treaties operational in their own national legal system.

inbreeding

The mating of individuals with close relatives, with whom they may share many genes.

inbreeding coefficient

The probability that two alleles at the same locus in an individual are identical by descent.

inbreeding depression

A sequence of events initiated by matings between closely related individuals, especially in small populations of normally outbreeding species, whereby heterozygosity and fecundity are reduced and mortality is increased through expression of deleterious, recessive alleles.

incidental take – *See also* taking
Under the US Endangered Species Act, harm or harassment done to a protected species that is incidental to, and not the purpose of, carrying out an otherwise lawful activity.

indicator species – *See also* surrogate species
A species whose conservation status is assumed to reflect the status of other species with which it shares the community.

instrumental value
The value of something that is realized through its usefulness, utility, or instrumentality to meet the needs or promote the good of another; a value that is realized in an object or entity through its use for some other purpose.

integrated conservation and development projects (ICDPs)
Projects in which local people share benefits of using or harvesting plant or animal resources in their environment at sustainable levels, take ownership of the conservation of such resources, and have an active role in decisions affecting the use and management of these resources in ways that benefit them individually and culturally. ICDPs generally attempt to achieve conservation as an outcome of sustainable community development rather than through exclusive focus on management or protection of the resource to be conserved.

integrodifference equation (IDE) models
A category of models that describe the predicted spread of an invasive species by breaking dispersal and population growth into separate stages.

international habitat reserve programs (IHRP)
A type of payment for environmental services (PES) program in which a system of institutional arrangements facilitate conservation contracting through multiple individuals or groups that supply ecosystem services. IHRP contracts specify that outside agents will make periodic performance payments to local actors if a targeted ecosystem remains intact or if target levels of wildlife or biodiversity are found in the ecosystem.

interventionist approaches
In invasive species management, management practices that attempt to control, reduce, or eradicate an invasive species after it has entered the system by intervening in or interfering with processes that permit its continued spread or persistence.

intrinsic coadaptation – *See also* outbreeding depression
A condition in which genes in a local population primarily adapt to the genetic environment defined by other genes, thereby creating an increased risk of a decline in fitness when breeding occurs with individuals from other populations (outbreeding depression). Intrinsic coadaptation can become especially prevalent in species that become subdivided into small, isolated populations.

intrinsic value
The value of something in and of itself, without regard to its usefulness or utility to others.

introgression
The long-term acquisition and incorporation of genetic material from one species into the genome of another species, especially when individuals of a rare species hybridize with those of a closely related, but more numerous species.

isolation model
A type of model predicting population distribution that assumes that changes in distribution are influenced primarily by distances between suitable habitat patches relative to dispersal abilities of the species.

J

Judeo-Christian Stewardship Environmental Ethic
An organized system of values for environmental care based on principles taught in the Old and New Testaments of the Bible, including especially a view of the intrinsic goodness of created things, the responsibility of human beings to care for and protect the non-human world, and the inclusion of non-human creation in the redemptive plans and purposes of God.

K

keystone species – *See also* function-based indicator species
A species with strong effects on community or ecosystem processes and biodiversity.

kinship coefficient
A measure of the degree of relatedness between two individuals, expressed as the probability that alleles randomly selected from homologous loci in such individuals are identical by descent from a common ancestor.

L

landscape
An area that contains discrete, distinct habitat patches.

lethal genes
Genes which, although recessive and unexpressed in a heterozygous state, will, in a homozygous condition, result in the death of the individual.

lethal load
The proportion of lethal genes in a population, which often rises when alleles are lost during a period of population reduction.

life table
A tabulation of age-specific rates of birth, mortality, survivorship, fecundity, and other population parameters that is used to identify the traits of populations that determine patterns of growth over time.

limit indicators – *See also* performance indicators
In ecosystem management, variables that detect or foretell a point at which a critical resource begins to come under stress. When the level of the variable reaches a pre-determined threshold or critical value, the manager is facing an unacceptable risk of harm to the resource or the system that produces it and should take immediate action.

limited access
A mitigation strategy designed to reduce the effects of human activity and movement to and from sites within wildlife habitat by restricting use of roads to the site as well as actual use of the site to essential activities performed by a relatively small number of designated individuals.

living modified organism (LMO) – *See also* genetically modified organism (GMO)
An organism whose genomes have been engineered or "spliced" so as to incorporate genes from other, usually very different, kinds of organisms in order to preserve, enhance, or add traits favorable to increased production, fertility, survivorship, or adaptability to particular environmental conditions.

logistic growth
A model of population growth in which population size increases at a decreasing rate as it approaches an upper asymptote, set by environmental limits.

M

mariculture
The intensive commercial cultivation of certain species in limited areas in a marine environment for eventual harvest as a "crop" for food or other resources.

market goods
Things that can be traded in standard currencies of exchange, such a money, in normal arenas of exchange, such as markets.

maximum-avoidance-of-inbreeding (MAI) strategy
A strategy of captive breeding management which avoids mating between relatives. In an MAI strategy, managers examine kinship between potential mates, which is equivalent to the inbreeding coefficient of potential offspring of the pair, and pair individuals with little or no kinship to one another (i.e., pairings that produce offspring with a low or zero inbreeding coefficient).

maximum sustained yield
The largest amount or level of removal of a particular resource from a system that can be taken indefinitely for successive time increments without depletion of the resource or loss of productivity of the system. If correctly determined, the maximum sustainable yield is equal to the regenerative rate of the resource in that system in each time increment.

mean generation time
The average age at which animals produce offspring.

mean kinship
The average kinship between a single individual and all other individuals in the population.

mean kinship (MK) strategy
A strategy of captive breeding management in which individuals with similar mean kinship values are paired for breeding, especially if such values are low, leading to the production of offspring with an increased representation of rare alleles.

mentor
A trusted counselor, guide, tutor or coach, particularly in one's own profession, who takes active interest in the welfare, development, and advancement of a younger or less experienced colleague or student.

metapopulation
A population that exists as spatially disjunct subunits at different densities in habitat patches of varying carrying capacity.

metapopulation theory
A conceptual model to describe collections of subpopulations of a species in a given area, each occupying a suitable patch of habitat in a landscape of otherwise unsuitable habitat.

microsatellites
A type of satellite DNA that consists of short tandem repeats 2–4 nucleotides long, and whose variability is useful in determining pedigrees of individuals.

minimum viable population (MVP)
The minimum number of individuals required for a population to persist for a specified length of time at a specified level of probability.

mining of legacy data – *See* data mining

minisatellites
A type of satellite DNA that consists of sequences up to 100 base pairs long, and whose variability forms the basis for DNA fingerprinting.

mitigation
In conservation, the lessening of the effects of human disturbances on populations, habitats, and landscapes.

movement rules
Rules used in landscape models which specify the distance across which sites are accessible to organisms by virtue of their dispersal or gap-crossing abilities.

moral agent
An entity capable of discerning between right and wrong, and therefore considered morally responsible for its actions and their consequences.

moral subject

An entity that can be treated rightly or wrongly in a moral sense, even though the entity itself might not be not capable of acting in a morally right or wrong manner.

multiple-use

A management approach, initially developed and practiced by the US Forest Service, that manages lands and ecosystems for multiple objectives simultaneously, such as wildlife conservation, timber production, and human recreational opportunity.

multiple-use module – *See also* zonation management

An approach to habitat conservation in which a fully protected core area is surrounded by concentric zones of natural areas used in progressively more intense fashion for recreation and commodity production.

N

natural catastrophes

Extreme forms of normal environmental variation (e.g., flash floods or severe and prolonged drought) that have the potential to eliminate all individuals in a small population.

naturalistic fallacy

The error of arguing for an imperative conclusion or normative action based on a descriptive premise; arguing from "what is" to "what ought to be." In science, attempting to prove an imperative or ethical conclusion based on a fact of nature.

neighborhood rules – *See* movement rules

neutral landscape models

A landscape model in which the distribution of habitats in the landscape is a theoretical distribution of habitat independent of (i.e., "neutral" toward) actual biophysical processes that shape landscapes.

niche assembly theories

Theories of ecological community composition which assert, in various ways and at various temporal and spatial scales, that different species are able to persist together in a community only if they differ sufficiently in niche separation (i.e., resource use).

no surface occupancy

A method of mitigation, often used in mining and drilling operations, in which humans do not extract resources directly from beneath high quality habitat, but remove the resources through directional (side) drilling from a more remote site in a lower-quality habitat.

no-take zones – *See also* harvest refugia

In marine environments, areas designed to protect a particular commercial stock or group of stocks from over-exploitation by prohibiting any harvest (i.e., "take") within the designated zone.

non-excludable goods and services

Goods and services for which it would be extremely difficult and costly to exclude anyone from receiving the benefits (e.g., protection from ultraviolet radiation by the ozone layer).

non-rival goods and services

Goods and services whose use by one person does not reduce or restrict use by others (e.g., breathing oxygen from the atmosphere).

non-spatial models

Models in which knowledge of spatial locations of entities of interest is not known, nor are processes and transfer rates affecting movement from one point to another. Nonspatial models are often used to predict the spread of invading organisms by using projections derived from population demography, such as exponential or logistic growth equations, or to predict changes in numbers of the invasive species through time.

null model

Models, particularly in population demography, that assume that changes in the variable of interest reflect random events.

O

occupancy model

Another name for the Levins' metapopulation model, based on its assumption that patches are either occupied (at carrying capacity) or unoccupied (no individuals in the patch).

oligonucleotide

A short piece of DNA used in the polymerase chain reaction.

opportunity cost

The best alternative that is given up or lost when a choice is made. For example, costs or losses associated with the inability to use a resource to produce goods A, B and C if the resource is used to produce good D.

optimal niche gestalt

An approach to habitat management, based on the idea that identifiable structural features of an environment allow a species to thrive, rather than merely persist.

option value

The value of a resource's expected future use, or what a person would be willing to pay to guarantee that the resource would be available for future use.

outbreeding depression

A decline in fitness that occurs when individuals from normally inbreeding populations breed with individuals from other populations of the same species, breaking up uniquely coadapted genetic combinations and resulting in subsequently reduced fitness and fecundity.

P

panmictic index

A measure of inbreeding as a deviation from the heterozygosity frequency expected under random mating. Expressed mathematically, the panmictic index, f, is

$$1 - H_o / H_e,$$

where H_e is the expected heterozygosity under random mating and H_o is the observed heterozygosity in the population.

parameters – *See also* converters
In a model, values of variables that determine rates of flow or movement of resources or individuals from one state to another or from one area to another.

partnerships
In ecosystem management and conservation, dynamic relationships among actors with vested interest in a system or resource based on mutually agreed objectives and pursued through an understanding of division of labor based on the respective comparative advantage of each member.

patch
The fundamental unit of a landscape, containing only one type of habitat.

patchiness
A quality of habitat arrangement, manifested as contrasting, discrete states of physical or biotic phenomena.

patch models
Models of habitat distribution or habitat use by organisms which arrange habitats in patches, i.e., small areas within landscapes which contain only one type of habitat.

pathway analysis – *See also* risk analysis
A management approach in which managers develop different management responses unique to particular pathways of movement or stages of population growth of a given species. Used particularly in the management of invasive species by seeking to control invasion rates through management responses unique to particular pathways and stages of invasion.

payments for ecosystem services (PES)
A conservation strategy in which an individual or group receives direct payment from a conservation organization or government agency for providing a specified, contracted ecosystem service, such as carbon sequestration, soil stability, or enhancement of site-specific plant or animal biodiversity, usually on land owned or controlled by the individual or group receiving the payment.

pedigree analysis
An analysis used in captive breeding and population management in which managers determine the relatedness of individuals in the population to one another by determining each individual's parental ancestry and subsequent offspring, and then use such analysis to inform choices of pairings for reproduction of new offspring.

pedigree inbreeding
Inbreeding by descent, or the measure of an individual's ancestry shared in its maternal and paternal lines.

pelagic species
In marine environments, free-swimming species that may disperse and move widely throughout ocean waters.

percolation cluster
In habitat and landscape ecology, a single group of habitat patches in sufficient proximity to one another such that organisms can move throughout the entire system (i.e., "percolate" from patch to patch).

percolation theory
Originally a theory of physics to describe and explain the physical properties of gels, polymers, and glassy materials, particularly as a means to understand the flow of liquids through material aggregates. In conservation biology, a theory of landscape ecology that provides a quantitative analysis of habitat connectivity in spatially structured landscape systems to describe and explain rates and types of movements of organisms between habitat patches or other elements.

percolation threshold
The level of disturbance in a landscape (e.g. the proportion of sites destroyed) at which the transition from a connected to a disconnected landscape system occurs. Above the threshold value, the landscape is considered to be connected (i.e., to consist of a single cluster of habitat spanning the entire system); below the threshold, the landscape is considered to be disconnected and to consist of numerous small clusters of similar but isolated habitat.

performance indicators
In ecosystem management, variables used to monitor the state or performance of an ecosystem, such that when the variable reaches a critical state or value, it triggers a predetermined management action.

performance payments – *See also* payments for ecosystem services (PES)
In conservation, an arrangement in which money is given directly to individuals or communities for meeting specified conservation objectives.

persistence likelihood
An estimate of the probability of persistence or extinction of a population, often determined as an outcome of a population viability analysis (PVA).

phenomenologically significant animals
Animals that evoke strong emotional or empathetic responses in humans.

Phylocode
A taxonomic system in which organisms are arranged in groups possessing shared characteristics (clades) and species names are assigned based on the shared ancestry of the clade to which the species belongs.

phylogenetic diversity index
A measure of diversity which incorporates known information about the evolutionary history and phylogeny of a taxonomic group, and thereby permits a way of estimating the taxonomic uniqueness or distinctiveness of each individual unit, such as species.

phylogenetic species concept
The idea that species should be defined by measuring genetic similarities, differences, and distances among populations or groups of populations. A species, according to a phylogenetic species concept, represents a group of organisms with an assumed or determined common ancestral lineage whose genetic similarities, differences, and distances are distinguishable from other such groups.

policy
A set of principles and intentions used to guide decision making; in environmental conservation, a set of principles and intentions used to guide decision making about human management of natural capital and environmental services.

polluter pays precautionary principle
The principle that, if uncertainty exists regarding the environmental effect of a proposed activity and its pollution potential, the potential polluter pays in advance for the possible costs of remediation and restoration, with the payment to be returned if no pollution occurs.

polluter pays principle
Economic strategies based on the principle that polluters (rather than society) should pay for the pollution they create, thus preventing polluters from externalizing pollution costs. Mechanisms associated with such strategies can include pollution-specific fees, taxes or fines assessed on a polluter for exceeding prescribed pollution limits.

polymerase chain reaction (PCR)
A genetic technique that uses DNA polymerase to repeatedly copy (amplify) a short region of a DNA molecule for various types of analysis, such as direct sequence of the PCR products to determine genotypes of individual animals.

polymorphism
A genetic locus that has two or more forms (alleles). In a population or population subunit, polymorphism is expressed as the probability of encountering a polymorphic loci among all loci in the population.

population
A group of individuals of the same species that is spatially, genetically, or demographically discontinuous with other groups.

population bottleneck
A drastic, temporary reduction in population size through catastrophe or dispersal of individuals to a new area, resulting in loss of genetic variation.

population mean kinship
The arithmetic mean of all individual mean kinships in a population.

population viability analysis (PVA)
The use of analytical or simulation models to make precise estimates of the likelihood of species persistence within a defined time period at a given level of probability, and to identify and rank or weight threats to such persistence from specific causes.

positivist view
In law, a paradigm of understanding law and its functions as neutral rules that are to be enforced by governing authorities.

precautionary principle
The principle that if the environmental outcome of a proposed action is uncertain, managers should err on the side of caution and place the burden of proof on the potential polluter to demonstrate that the activity will not do irreversible harm to the environment or its long term conservation.

primary environmental ethic
An organized system of values that treats environmental entities, such as non-human creatures or natural objects, as moral subjects that can be treated or used rightly or wrongly by humans, and thus the primary benefactors or victims of ethical decisions affecting their welfare.

private goods
Goods that can be bought, sold and enjoyed individually by private buyers and sellers, and which can be used and enjoyed by an individual in such a way that the individual can exclude others from the use or enjoyment of the good.

process view
In law, a paradigm of understanding law and its functions as normative frameworks and procedures for coordinating behavior, controlling conflict, facilitating cooperation and achieving values. Compared to the positivist view of law, the process view understands laws to be effectual primarily through moral and social support of the principles they embody, not by enforcement from governing authorities.

professional advocacy
The act of informing policy makers, managers and the public about issues that arise in one's area of expertise through publication in scientific and professional books and journals, and avoiding other, more direct or personal methods of information transfer.

protectionist approaches
In the management of invasive species, management strategies that focus on preventing non-native species from entering the system, and emphasize monitoring and surveillance at potential entry points to prevent the introduction of a non-native species.

public goods
Goods that are not easily transacted between individual buyers and sellers, and that can be used and enjoyed by all in such a way that no individual can easily exclude others from the use, benefit or enjoyment of the good.

public trust
A legal doctrine, originally attributed to the Roman Emperor Justinian, that asserts that governments hold certain rights and entitlements in trust for the people and are therefore obligated to protect those rights for the common good;

often applied to natural resources such as air, water, seashores, forests or other types of habitats and ecosystems.

Q

quasi-option value
The value of preserving options for future use, given an expectation of growth in knowledge or applied technology that might lead to a future, but as-yet undiscovered or unrealized use for the resource.

R

radiative forcing
A change in the energy balance of the earth-atmosphere system in response to a change in factors such as greenhouse gases, land-use change, or solar radiation. Positive radiative forcing refers to an increase in the temperature of a system, such as the atmosphere, that occurs as a result of absorption of energy, while negative radiative forcing refers to changes in the system that create cooling.

random amplified polymorphic DNA (RAPD) analysis
A genetic technique that requires only a small amount of material from a living creature (e.g., discarded hair, feathers, antlers or eggshells) and uses one random oligonucleotide primer to generate essentially unlimited numbers of loci for analysis.

reaction-diffusion model
A type of species invasion model in which populations travel as a wave of a given velocity (V) determined by the population's intrinsic rate of increase (r) and rate of movement or distance traveled (D), expressed as

$$V = 2\sqrt{rD}.$$

reclamation
The preparation and enhancement of degraded land to fulfill its former use or a new use.

recruitment
The entry of young organisms into a population.

Resource Conservation Ethic
A view, popularized by Gifford Pinchot, that the highest and best use of nature was the management of its resources in the most efficient way to achieve the greatest human good for the greatest number of people in both present and future generations.

restriction fragment length polymorphisms (RFLPs)
Variations in the length of restriction fragments produced from identical regions of the genome which can be used to measure variation in nuclear DNA among individuals.

revealed preference methods
A family of behavior-based, analytical economic techniques that attempt to use metrics associated with specific preference-driven behaviors, such as costs associated with travel to a site for a particular activity, to determine the value associated with a user's preferences for such activity.

risk analysis – *See* pathway analysis

rival goods
Goods whose consumption or use by one person reduces the amount available for everyone else.

Romantic Transcendentalism
A view, popularized by Ralph Waldo Emerson, Henry David Thoreau and other US essayists and philosophers that the highest and best use of nature was as a place of spiritual renewal, moral formation and encounter with the divine.

rule-based model
A type of model used to evaluate possible mechanisms of distributional changes in species or habitat distribution using predetermined rules of movement, habitat selection or habitat or landscape succession patterns.

S

safe harbor agreement – *See also* habitat conservation plan (HCP)
A type of habitat conservation plan (HCP) under which a landowner agrees to actively maintain suitable habitat ("safe harbor") for a predetermined number of a species equal to the number present on the site when the agreement is formulated. In return, the landowner receives an incidental take permit that authorizes future land-use changes or management on other parts of the site that may be occupied by additional individuals of the endangered species, and removes liability for harm to those individuals of the species incurred from the authorized activity of the landowner.

satellite DNA
Short, highly repetitive segments of DNA in an organism's genome with base sequences differing from those of other forms of DNA.

secondary environmental ethic
An organized system of values that treats environmental entities, such as non-human creatures or natural objects, as morally neutral agents or means to advance human welfare, such that the ethical consideration of the effect of any decision on the condition or welfare of natural objects or non-human species is secondary to ethical considerations of its effect on humans.

sex ratio
The ratio of males to females in a population.

simulation model
A model that provides mathematical estimation of the state of a system through time and, in landscape and ecosystem management contexts, across space.

sink
In a metapopulation, an area of low-quality habitat in which the population cannot replace itself without immigration.

small population paradigm
A general theory of the characteristics of small populations, causes and effects of threats to small populations, and how those threats can be managed.

soft law
In the context of international law, nonbinding agreements that, although having no official means of enforcement, eventually come to define the norms and standards for international behavior among nations.

source
In a metapopulation, an area of high-quality habitat in which population surpluses are produced which provide a source of individuals to colonize new areas or habitat patches.

spatially explicit model
A metapopulation or landscape model that incorporates differing degrees of connectedness between population or landscape subunits and features localized interactions between subunits or individuals whose rules are defined by the spatial relationships between interacting agents.

spatially implicit model
A metapopulation model (e.g., Levins' model) or landscape model in which habitat patches and local populations are discrete, but equally connected with one another.

spatially realistic model
A metapopulation model that incorpo rates the specific geometry (e.g., size, shape, and arrangement) of particular patches.

spatial scale
A measure of habitat patchiness that relates interpatch distance to a species' dispersal ability.

species–abundance curve
The graphical representation of a species–area relationship.

species–area relationship
The relationship between the number of species present in an area and the size of the area, mathematically expressed as the basic equation of the Equilibrium Theory of Island Biogeography, $S = cA^z$, which describes the number of species on an island (S) as a constant power of the island's area (A), mediated by two constants, c and z, where c is a constant specific to a particular taxonomic group and z is an "extinction coefficient" which integrates the rate of extinction in that group to the number of species associated with the area. In most cases the species-area relationship is direct-linear, with species increasing in number with increasing area at a relatively constant rate.

species list
A list of species present in a community.

species richness
The number of species present in a community standardized to reflect the number of species recorded per sampling area or observation effort.

stakeholders
Individuals or groups possessing vested interests in the persistence, health, products, state or services of a system to whom managers have legitimate and defined functional, ethical, legal or contractual obligations.

stasis rate – *See also* transition matrix
The diagonal elements in the matrix of present conditions (rows) and future conditions (columns) that represent the proportion of cells of life stage (for populations) or habitat type (for landscapes) that do not change from the present to the future.

stepping-stone model
A model of metapopulation gene flow that assumes that populations, and the genes they carry, move or disperse only a single step ("one step at a time") among population subunits in each generation, thus requiring many generations for an introduced allele to move through all segments of a large population.

stochastic factors
Factors whose effects on a population vary randomly, but usually within a limited range.

stock
A standing crop or source from which a resource originates or is produced by ecological processes.

stock-flow resources – *See also* fund-service resources
Resources, usually produced from a standing crop or "stock," that are materially transformed into a new kind of material which they produce, can be used at any rate desired, and whose production is measured as a quantity of output produced. Forage for herbivores produced by a grassland is an example of a stock-flow resource.

stratified diffusion model
A type of species invasion model that incorporates long-distance dispersal and density dependent rates of spread.

structure-based indicators
Indices of changes in biodiversity calculated through assessment of changes in ecological structure, such as forest stand complexity or foliage height diversity.

succession model
Models of organism distribution that assume that such distributions are determined by changes in vegetation or other environmental qualities which change over time.

sunshine approach
An approach to international treaty enforcement which focuses on mechanisms to bring the behavior of key parties (usually nation states) into the open for public scrutiny, including such actions as regular reporting, peer scrutiny, on site monitoring and media access and coverage.

surrogate species – *See also* indicator species
A species whose status is assumed to reflect the status of other species with which it shares the community.

sustained yield
The amount of an exploited population that can be harvested in a present time increment leaving the population's productivity undiminished in future time increments.

T

taking
In the context of traditional property law, hunting, fishing, collecting, or trapping a creature to kill it or bring it into personal possession. Under the US Endangered Species Act, the traditional concept is expanded to include any intentional or unintentional act that harms or harasses a protected species in any way.

target indicators – *See also* performance indicators.
In production-oriented ecosystem management, variables that measure outputs of what the system is intended to produce, such as a specified level of stock or biomass of a particular resource.

target population size
The population size at which managers attempt to maintain a captive population.

teleology
A system of ethics that gives primacy to the outcomes that can be expected from an action, such that moral decisions are based on actions which achieve the "best" outcomes and anticipated future conditions.

temporal scale
In the context of habitat conservation, the duration of a habitat relative to a species' generation time. More generally, the units and anticipated span of time appropriate to an object of investigation.

timing limitations
A method of mitigation limiting human activities in habitats which are seasonally or periodically occupied by wildlife to those seasons or times when wildlife are absent.

transition matrix
In population viability analysis or habitat successional analysis, an arrangement of rows and columns that display the probability of an individual at one life stage or habitat type in the present (column headings) changing or transitioning into a new life stage or habitat type in a subsequent time period (row headings).

travel cost method (TCM) – *See also* revealed preference methods
A method of determining the values of environmental amenities, goods and services based on the assumption that the more valuable an environmental amenity, good or service, the farther people are willing to travel to get it, the more they will spend per trip, and the more trips they will make.

trend analysis
A population monitoring tool for calculating one or more specific demographic variables in a population and, based on the value of the variable, then determining whether the population is growing, stable or declining.

turtle excluder device (TED)
A grid trapdoor installed inside a shrimp trawling net that keeps shrimp in the net but directs other, larger animals, such as sea turtles, out.

typological species concept
The idea that species are distinguished by morphological characteristics that can be determined by gross observation.

U

umbrella species
A species, or group of species (e.g., large mammals), of particular conservation or public interest, and whose protection is assumed to provide benefit or a protective "umbrella" to many other species in other taxonomic categories.

unified neutral theory of biodiversity and biogeography
The theory that ecological communities are open, non-equilibrium assemblages of species that are only weakly competitive or co-adapted. The presence, absence and relative abundance of species are assumed to be dictated by random speciation, dispersal, ecological drift (a form of demographic stochasticity, the random variations in a population's rates of birth and death) and extinction. Processes affecting demographic variables in every species in a trophic group, such as rates of birth, death, migration and speciation, are "neutral" in that they affect every individual with the same proportional weight.

use value
The value derived from the actual use of a resource.

V

value
The basis for an estimation of worth.

veligers
Free-swimming, filter-feeding larvae of molluscs, such as the zebra mussel (*Dreissena polymorpha*).

visual minimization
A method of environmental mitigation that involves reducing the distance at which animals can see objects associated with human disturbance.

W

wetland
An area or ecosystem in which the water table is at or near the surface or the land is covered by shallow water during at least part of the year, vegetation is dominated by hydrophytic (literally, "water-loving") plants, or the substrate is characterized by hydric (wet or waterlogged) soil types.

wilderness ideal
The view that large landscape areas relatively unaffected by human activity or residence represent ideal ecosystems that should be given priority in nature conservation and preservation in order to better study their ecological processes and conserve their species components.

Willingness to Accept Compensation (WTC)
A form of contingent valuation (CV) analysis in which the market value of a non-market good, such as a non-human species, is estimated by what a person would be willing to accept as compensation for its loss.

Willingness to Pay (WTP)
A form of contingent valuation (CV) analysis in which the market value of a non-market good, such as a non-human species, is estimated by what a person would be willing to pay to prevent its loss or harm.

Y

Yellowstone Model
A pattern of establishing national parks based on the characteristics of Yellowstone National Park, USA, emphasizing the conservation of regional-scale landscape areas characterized by relatively little human impact and residence, or the removal of resident humans and their activities and impacts from such areas if necessary to fulfill conservation objectives.

Z

zonation management – *See also* multiple-use module (MUM)
The management of an area through the use of different policies and procedures applied to different portions (zones) of the area, often with the least intrusive or disruptive management applied to inner or "core" regions, and increasingly intrusive management of resources or control of populations in outer areas.

zoning – *See also* conservation easement
An arrangement in which some of the property rights normally associated with the individual owner of a property are transferred to or held by the community in which the property is located, effectively restricting what individual property owners can do on their property because of the context in which the property is located. Conservation easements are a special case of zoning applied toward conservation objectives.

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