

# ANIMAL MINDS



Donald R. Griffin

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## P R E F A C E

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This book will review evidence of versatile thinking by animals, and of equal significance will be a representative sampling of the wide range of scientific and scholarly opinion about animal minds. This spectrum of strongly advocated views demonstrates the basic importance attached to the nature of animal mentality by both scientists and philosophers. Cognitive ethology, the analysis of cognitive processes in nonhuman animals, has attracted thoughtful and constructive contributions from fields as diverse as behavioral ecology and the philosophy of mind. This has led to many significant discoveries about animal behavior and cognition. Many students of animal cognition avoid consideration of whether animal cognition is ever accompanied or influenced by conscious thinking. But because conscious awareness adds so much to an unconscious “sleepwalker” existence, it is important to consider the evidence suggesting both cognitive processes and conscious thinking.

Contemporary human thinking about animal mentality falls into three camps, although none is a monolithic dogma and all include many shades of opinion. The first, commonsense view is that animals are likely to think about what they are doing and the results they expect from their actions, especially when these are adapted to varying and often unpredictable circumstances. In stark contrast was the second position, that of the strict behaviorists, who used to argue that subjective mental experiences are inconsequential side effects that should be totally ignored by serious scientists. They attempted to explain all behavior, animal and human, exclusively in terms of external influences and how these affect overtly observable behavior.

Behaviorism was the dominant school of psychology for many years, but during the past generation psychology has undergone a “cognitive revolution” as most psychologists have adopted a third, intermediate position. They have abandoned the taboos of strict behaviorism and consider themselves cognitive psychologists because they recognize that



internal processes within brains or minds are of the utmost importance in determining the behavior of men and animals. These cognitive processes entail, among other attributes, representations, including memories, expectancies, and anticipations. Internal manipulations of such representations are held to result in decisions, and classification of objects in relation to desires and beliefs. That is, animals want some things, fear others, and expect that actions will lead to certain results.

Yet cognitive psychologists are very suspicious of claims that animals are conscious, even when they recognize that cognition must be assumed in order to explain the animal's behavior. Because the vast majority of human brain functioning occurs without our conscious awareness, it is possible that all animal behavior is unconscious. Because evidence for or against animal consciousness has been difficult to evaluate by scientific methods, the contemporary view of many cognitive psychologists can be summed up as: "Animal cognition: yes of course; but animal consciousness: unlikely, or, if it does occur, impossible to detect, since whatever the animal does might be done unconsciously."

This intermediate position of contemporary cognitive psychologists is a great advance, but the reluctance to move ahead from cognition to consciousness may well be a lingering residue of behaviorism. Many cling to the positivistic view that, in the words of Latta (1986, 309, 313), "Conscious awareness in other animals is a closed world about which we can do no more than speculate. . . . Sadly for those of us who agree (that studying the subjective experiences of animals would be a desirable goal), there is no evidence that it is anything but unattainable." This antipathy to consideration of consciousness threatens to become a sort of self-inflicted paralysis of inquiry, an obsolete hindrance to scientific investigation. For no one seriously doubts that human conscious thinking is real and important, or that it sometimes influences our behavior. Why then is it out of the question to learn whether nonhuman animals think consciously? The usual answer to this question is that other people can tell what they are thinking or feeling, but no such evidence is available about any conscious thoughts that might conceivably be experienced by animals.

Insofar as animals do experience conscious thoughts, it must often be important to convey them to companions, rivals, or even members of other species. Charles Darwin and many other students of animal behavior have interpreted animal communication as expression of emotions, but ethologists have recently discovered that some animals express both feelings and simple thoughts. These communicative signals

in turn provide us with a promising source of objective data about the mental experiences of nonhuman animals. We can record and analyze them; and we can learn from the responses of recipients a great deal about what messages they convey. Experimental playback of recorded signals is often helpful in identifying what specific information they convey. Just as human speech, along with nonverbal communication, tells us most of what we know about the thoughts and feelings of other people, so the scientific analysis of animal communication provides us with a useful window on animal minds.

Furthermore, animals often behave in such a versatile manner that it seems much more likely than not that they experience simple conscious thoughts about their activities, even when these are not expressed by specific communicative signals that we can recognize. Analysis of behavioral versatility can certainly lead to improved understanding of animal cognition. This cognitive approach to animal behavior can also serve as constructive compensation for the unfortunate tendency of many scientists to belittle nonhuman animals by underestimating the complexity and the capabilities of the animals they study.

There is considerable overlap with my two earlier books on the same general subject (Griffin 1981, 1984) because many examples of animal behavior suggesting cognition or conscious thinking are as pertinent today as they were ten or fifteen years ago. But a number of additions, corrections, and revised interpretations are now needed to take advantage of significant new ideas and critical formulations which have clarified many relevant issues. The renewed interest in animal cognition and intelligence is abundantly demonstrated by numerous recent books and articles, many of which will be discussed in the following chapters. But this interest has produced far more scholarly books and articles than can be adequately reviewed in one volume. I have therefore selected primarily the more recent publications, especially those with appropriate bibliographies.

I have been pleasantly surprised to find how enlightening it is to review the extensive published literature on animal behavior from this cognitive perspective. As even two of the most severe critics of this approach have recognized, "the development of cognitive ethology has helped emphasize that animals routinely engage in behavior more complex than most ethologists or psychologists would have thought plausible" (Yoerg and Kamil 1991). Thus we can at least hope to learn just how versatile animals actually are by considering what is known of their behavior from what seems likely to be their own perspectives (Griffin

1990, 1991). And, furthermore, I expect that we will find it more and more plausible that animals are sometimes consciously aware of their situation and of the likely results of their activities.

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## *Animal Mentality*

**M**ental experiences are real and important to us, and insofar as they occur in nonhuman animals they must be important to them as well. They are certainly important to our appreciation of animals, for we can only understand other species fully when we know what, if anything, they think and feel. It is therefore important for those interested in animals to learn as much as possible about whatever thoughts and feelings they experience. Unfortunately, almost all of the scientists who study animal behavior avoid this subject; and many deny the existence or the significance of animal consciousness. Because it is so difficult to prove rigorously whether any given animal is conscious, no matter how ingenious its behavior, scientists have tended to cling to the conservative assumption that all animal behavior is *unconscious*. But recent discoveries about animal behavior have rendered this tendency to minimize the implications of animal versatility more and more difficult to maintain. The dilemma faced by the conservative “nothing but” position preferred by many scientists is illustrated by two examples.

A hungry chimpanzee walking through his native rain forest in the Ivory Coast, comes upon a large *Panda oleosa* nut lying on the ground under one of the widely scattered Panda trees. He knows that these nuts are much too hard to open with his hands or teeth, and that although he can use pieces of wood or relatively soft rocks to batter open the more abundant *Coula edulis* nuts, these tough Panda nuts can only be cracked by pounding them with a very hard piece of rock. Very few stones are available in the rain forest, but he walks for about 80 meters straight to another tree where several days ago he had cracked open a Panda nut with a large chunk of granite. He carries this rock back to the nut he has just found, places it in a crotch between two buttress roots, and cracks it open with a few well-aimed blows. (The loud noises of chimpanzees cracking nuts with rocks had led early European explorers

to suspect that some unknown native tribe was forging metal tools in the depths of the rain forest.)

In a city park in Japan, a hungry green-backed heron picks up a twig, breaks it into small pieces, and carries one of these to the edge of a pond, where she drops it into the water. At first it drifts away, but she picks it up and brings it back. She watches the floating twig intently until small minnows swim up to it, and she then seizes one by a rapid thrusting grab with her long sharp bill. Another green-backed heron from the same colony carries bits of material to a branch extending out over the pond and tosses the bait into the water below. When minnows approach this bait, he flies down and seizes one on the wing.

Must we reject, or repress, any suggestion that the chimpanzee or the heron thinks consciously about the tasty food it manages to obtain by these coordinated actions? Many animals adapt their behavior to the challenges they face either under natural conditions or in laboratory experiments. This has persuaded many scientists that some sort of cognition must be required to orchestrate such versatile behavior. For example, in other parts of Africa chimpanzees select suitable branches from which they break off twigs to produce a slender probe, which they carry some distance to poke it into a termite nest and eat the termites clinging to it as it is withdrawn. Apes have also learned to use artificial communication systems to ask for objects and activities they want and to answer simple questions about pictures of familiar things. Vervet monkeys employ different alarm calls to inform their companions about particular types of predator.

Such ingenuity is not limited to primates. Lionesses sometimes cooperate in surrounding prey or drive prey toward a companion waiting in a concealed position. Captive beaver have modified their customary patterns of lodge and dam building behavior by piling material around a vertical pole at the top of which was located food that they could not otherwise reach. They are also very ingenious at plugging water leaks, sometimes cutting pieces of wood to fit a particular hole through which water is escaping. Under natural conditions, in late winter some beaver cut holes in the dams they have previously constructed, causing the water level to drop, which allows them to swim about under the ice without holding their breath.

Nor is appropriate adaptation of complex behavior to changing circumstances a mammalian monopoly. Bowerbirds construct and decorate bowers that help them attract females for mating. Plovers carry out injury-simulating distraction displays that lead predators away from their eggs or young, and they adjust these displays according to the

intruder's behavior. A parrot uses imitations of spoken English words to ask for things he wants to play with and to answer simple questions such as whether two objects are the same or different, or whether they differ in shape or color. Even certain insects, specifically the honeybees, employ symbolic gestures to communicate the direction and distance their sisters must fly to reach food or other things that are important to the colony.

These are only a few of the more striking examples of versatile behavior on the part of animals that will be discussed in the following pages. Although these are not routine everyday occurrences, the fact that animals are capable of such versatility has led to a subtle shift on the part of scientists concerned with animal behavior from assertions that animals do not think at all to the view that their thoughts are very different from ours. For example, Terrace (1987, 135) closes a discussion of "thoughts without words" as follows: "Now that there are strong grounds to dispute Descartes' contention that animals lack the ability to think, we have to ask just how animals *do* think." Because so many cognitive processes are now believed to occur in animal brains, it is more and more difficult to cling to the conviction that none of this cognition is ever accompanied by conscious thoughts. The aim of this book is to reopen the basic question of what life is like, subjectively, to nonhuman animals, and to outline how we can begin to answer this challenging question by analyzing the versatility of animal behavior, especially the communicative signals by which animals sometimes appear to express their thoughts and feelings.

Many scientists feel that terms such as mind or consciousness are too vague and slippery to be useful in scientific investigation; and they often argue that these and other words describing subjective mental experiences cannot be defined with sufficient precision to allow objective testing of the presence or absence of whatever they designate. I will discuss definitions in greater detail later in this chapter and in chapter 12, but it is helpful to emphasize at the outset that the most basic and essential aspect of consciousness is thinking about objects and events. The content of conscious experience may ordinarily be limited to what the animal perceives at the moment about its immediate situation; but sometimes its awareness probably includes memories of past perceptions, or anticipations of future events. An animal's understanding may be accurate or misleading, and the content of its thoughts may be simple or complex. A conscious organism must ordinarily experience some feeling about whatever engages its attention. Animal feelings, and especially animal suffering, are recognized by most scientists as real and

significant (Bekoff and Jamieson 1990, 1991; Dawkins 1990). Furthermore, any thinking animal is likely to guide its behavior at least partly on the basis of the content of its thoughts however simple or limited such thoughts may be. Animals obtain most of the information that affects their behavior through their sense organs, including those that signal conditions within their bodies. But some mental experiences are probably based on past sensory input; and some may arise through recombination into new patterns of information already present in the central nervous system.

One reason to suspect that nonhuman animals do experience conscious thoughts is that the basic structure and functioning of neurons and synapses are quite similar, as far as we know, in all animals with organized central nervous systems. There is no convincing evidence that specific features of gross neuroanatomy are essential for conscious thinking. Therefore it is best to keep an open mind about the possibility of consciousness in all animals that exhibit versatile behavior or communicate in ways that suggest they may be expressing thoughts or feelings. We are consciously aware of only a small fraction of what goes on in our brains, and there is no reason to suppose that this fraction will prove to be larger in other species. The fact that we are unaware of so much that occurs in our brains has led many scientists to neglect consciousness because it is held to be an epiphenomenon or trivial by-product of neural functioning (Velmans 1991). But the component of central nervous system activity of which we *are* conscious is of special significance because it is what makes life real and important to us; and insofar as other species are conscious, the same importance may well be manifest. Animals may carry out much, or even perhaps all, of their behavior quite unconsciously, but insofar as they are conscious, their consciousness is an important attribute.

Whatever thoughts and feelings nonhuman animals experience may be quite different from ours, and presumably much simpler; but this does not mean that they are insignificant. There is of course no reason to suppose that other animals are capable of the enormous variety of thinking that our species has developed, largely through the use of our magnificent language—especially written language that allows the dissemination and preservation of knowledge far beyond what can be achieved by direct communication and individual memories. Animal thoughts probably concern matters of immediate importance to the animals themselves, rather than types of thinking that are primarily relevant to human concerns.

I will take it for granted that behavior and consciousness in both

animals and men result entirely from events that occur in their central nervous systems. In other words, I will operate on the basis of emergent materialism as defined by Bunge (1980, 6), and assume that there are no immaterial, vitalistic, or supernatural processes involved in the small fraction of human or animal brain events that result in conscious, subjective thoughts and feelings. This approach differs from that of Sperry (1983), who appears to take the essentially dualistic position that consciousness is something different in kind from the physical world. But otherwise his thoughtful and idealistic analyses are quite consistent with the view that consciousness exerts a causal influence on brain function and behavior, and is not limited to our species. Because our own consciousness and thinking occur in an enormous variety of forms, these terms suggest different meanings to various people. Animal thinking and feeling may also be much more varied and subtle than anything I will discuss in the following pages; but in trying to ascertain whether animals experience any conscious thoughts at all, it is helpful to concentrate on simple and basic sorts of conscious thinking that are the least difficult to detect.

Recognizing our ignorance is a necessary first step toward reducing it. The customary view of animals as always living in a state comparable to that of human sleepwalkers is a sort of negative dogmatism. We know far too little to judge with any confidence when animals are or are not conscious, and it is just as difficult to disprove as to prove that a particular animal is thinking consciously. Thus the question of animal consciousness is an open one, awaiting adequate scientific illumination. Many behavioral scientists dismiss this effort as idle speculation; but speculation is where scientific investigation begins, and I hope to stimulate new and enterprising inquiries that will significantly reduce our current ignorance and aversion. Regardless of the degree to which it may come to seem more or less probable that various animals experience particular conscious thoughts and subjective feelings, this approach should open up significant but largely neglected opportunities to attain a fuller and more accurate understanding of the other creatures with which we share this planet.

There is little new about the basic question of what the mental experiences of animals may be; that question was articulated and debated by Darwin, Romanes, Lloyd Morgan, von Uexkull, and many other scientists of the nineteenth and early twentieth centuries who were deeply interested in animal mentality. The history of the debate has been thoroughly reviewed by many scientists, including Schultz (1975), Wasserman (1981) Boakes (1984), Dewsbury (1984), Richards (1987), and



especially by Burghardt (1985a, 1985b). Indeed the nature of animal minds was a major subject of investigation and discussion up to the 1920s and 1930s, when it was repressed by behaviorism's restriction of scientific attention to overtly observable behavior, as discussed later in this chapter. What *is* new is the accumulated results of half a century of active and successful investigation of animal behavior. This has now provided a wealth of data about the complexities and versatility of animal behavior under natural conditions, and what they can learn to do in the laboratory. We can therefore return to the investigation of animal minds with far better and more extensive factual evidence than what was available to nineteenth-century biologists.

Comparative psychologists, ethologists, and behavioral ecologists have come to call themselves behavioral scientists, both because they study behavior, and because they *avoid* considering subjective mental experiences. Therefore, most of the scientists who study animal behavior have had little or nothing to say about the feelings or thoughts of the animals that interest them so keenly; and in their writing one almost never finds any use of terms such as "think," "intend," "believe," and the like. Thus Colgan (1989) and Yoerg (1991) speak for many of their colleagues in adamantly eschewing any scientific concern with the mental experiences of animals. A primary reason for this avoidance of the subject is a belief that mental experiences, especially those of animals, are inaccessible to scientific investigation because they are private to the organism experiencing them. Hence it is claimed that no statement about them can be verified by others. But we do of course obtain useful if incomplete and somewhat distorted information about other people's thoughts and feelings by making inferences from their behavior, and especially their communicative behavior. Furthermore, the difficulty, or even the impossibility, of conveying to others the exact nature of something does not rule it out of existence or deprive it of significance. Many things have been profitably analyzed by scientists long before their nature could be defined in complete detail. It can be questioned whether any important scientific entity can be described with 100 percent completeness.

The taboo against considering subjective mental experiences of non-human animals has become a serious impediment to scientific investigation. Effective indoctrination—often accomplished by nonverbal signals of disapproval—inhibits students and young scientists from venturing into this forbidden territory, and those that do so encounter criticism and ridicule. One result is that students of animal behavior are inhibited from reporting versatile behavior that suggests conscious

thinking; and scientific journals sometimes refuse to publish data or interpretations that support the inference of animal consciousness (Searle 1990b; Whiten and Byrne 1988).

Some exceptions to this taboo against considering mental experiences of nonhuman animals have begun to appear in recent years—for instance, Crook (1980, 1983, 1987, 1988), Denton (1982), Barkow (1983), Staddon (1983), Burghardt (1985b, 1991), Oakley (1985), Knapp and Robertson (1986), Cheney and Seyfarth (1990a), and some, but by no means all, of the contributors to symposia edited by Weiskrantz (1985, 1988). The neurophysiologist Eccles (1989) is persuaded that at least simple mental experiences occur in birds and mammals, but not in insects. An important parallel development has been what is often called the “cognitive revolution” in psychology, by which the strict behaviorism advocated by B. F. Skinner has been largely replaced by concern with cognitive processes, that is, internal representations in the brain and how their interactions affect overt behavior, as discussed in more detail in chapter 6.

The history of this cognitive revolution in psychology has been abundantly reviewed by Baars (1986, 1988), Gardner (1985), Miller (1988), and Riley, Brown, and Yoerg (1986), among others. An excellent perspective on contemporary thinking and controversies is presented in the book edited by Blakemore and Greenfield (1987). Numerous review articles, symposium volumes, and substantial books have been devoted to the cognitive psychology that has largely replaced behaviorism—for instance, Anderson (1983), Johnson-Laird (1983, 1987, 1988), Knapp and Robertson (1986), Marcel and Bisiach (1988), Newell (1990), and Whiten (1991). Even Pavlovian conditioning turns out to be much more complex than we used to take for granted and to entail learning of relationships rather than simple linking of specific stimuli with specific responses (Rescorla 1988; Gallistel 1990).

Analogies to computer systems have been central to this development, and a major reason for abandoning the inhibitions of behaviorism has been the ability of computer systems to perform many mental operations that used to require human thinking, as discussed in detail by Shallice (1978, 1988a, 1988b), among others. Since these information-processing devices can do so much, the overwhelming temptation has been to assume that human and animal brains and minds must operate in similar ways. As summarized by Riley, Brown, and Yoerg (1986, 115), “the rise of the computer as a metaphor has provided a rich source of ideas for how cognitive systems might operate. If

such ideas are compatible with phenomenology, so much the better. . . . Cognitive psychologists . . . are *methodological* behaviorists.” (Methodological behaviorism is the reliance on observations of behavior as data about internal mental states and processes without following the strict behaviorists in denying their existence or importance.) Many cognitive psychologists are thus persuaded that, in the words of Johnson-Laird (1988, 367), “the computer is the last metaphor for the mind.”

But this cognitive revolution in psychology has largely ignored the question which, if any, of the cognitive processes that are now freely postulated to occur in the brains of men and animals are accompanied by conscious awareness. A recent exception to this tendency is Baars (1988, 356), who writes at the conclusion of a chapter on the functions of consciousness: “Consciousness *is* special; but its wonderful qualities are not isolated from other realities; nor is biological usefulness a special virtue. Consciousness is the vehicle of our individuality, something that makes it of inestimable significance to us.” I will return to this topic later in this chapter, and in more detail in chapters 6 and 12; but first it is necessary to consider some basic problems that have deterred many behavioral scientists from seriously considering animal consciousness.

Many students of animal behavior are now quite willing to apply the terms “cognition” or “cognitive” to a wide variety of animals that perform adaptive and versatile behavior without concerning themselves with the question whether the animals are consciously aware of the information being processed by their nervous systems. For example, Wittenberger (1981, 48) has clearly expressed the prevailing viewpoint of most behavioral ecologists:

Cost-benefit analyses (are discussed) *as if* [italics in original] behavior results from a conscious decision-making process. . . . This procedure is just a short-hand logic used for convenience. We cannot assume that animals make conscious decisions because *we cannot monitor what goes on inside their heads*. Nevertheless, *it really does not matter* [italics mine] what the proximate bases of those decisions are when evolutionary reasons underlying the behavior are our principal concern. . . . The question of whether those choices are conscious or unconscious need not concern us, as long as we remember that our tacit assumptions about purposiveness are just that. . . . Particular stimuli or contexts elicit particular behaviors. An animal need not know why those stimulus-response relationships exist. It need only know what the relationships are. This knowing need not involve conscious awareness, though in many cases animals are undoubtedly conscious of what they are doing; it need only involve the appropriate neurological connections. . . . Animals can be goal-directed without being purposeful, and they can behave appropriately without knowing why.

Krebs and Dawkins (1984) have discussed animal communication from an evolutionary perspective emphasizing its function in (a) permitting one animal to manipulate others to its own advantage, and (b) what they call mind-reading. By "mind-reading" they mean prediction of one animal's behavior by another on the basis of the former's behavior, especially its communicative behavior. They emphasize the evolutionary advantages of manipulation and mind-reading by social companions and by both predators and prey. They avoid committing themselves "to a view over the philosophical problems of animal mind in the subjective sense." But they state that many ethologists have concluded that "animals respond in mechanical robot-like fashion to key stimuli," and they contend that "we should not ask whether the stickleback 'thinks' the (red) mail van is a rival." (This refers to the well-known observation by Tinbergen that red-bellied male sticklebacks when highly motivated to court females display aggressively towards very crude models of other males provided they have a red color.) Yet Krebs and Dawkins refer to animals as willing or unwilling participants in mind-reading interactions. In a similar vein Guilford and M. S. Dawkins (1991) discuss the psychology of animals receiving and reacting to communicative signals but avoid mentioning any subjective mental experiences of the animals whose psychology is under consideration.

Like most biologists, Krebs and Dawkins acknowledge that many animals are probably often conscious of what they do, but they turn away from the implications of this recognition and limit their consideration to the evolutionary adaptiveness of animal behavior. A primary reason is the conviction that "we cannot monitor what goes on inside their heads." Yet scientists have many ways of learning a great deal about what goes on inside the brains of animals. Neurophysiological data of the sort discussed in chapter 7 is one important source of relevant evidence. And mental imagery provides a good example of something that cannot be observed directly, but which cognitive psychologists have studied successfully by indirect methods, as reviewed by Hannay (1971), Haynes (1976), Finke (1989) and Kosslyn (1988). Similar approaches have begun to be employed to study imagery in animals by Rilling and Neiworth (1987). Farah (1988) has reviewed strong evidence that the same areas of the human brain are active when subjects think about something as when they are stimulated by it directly. Thus the reluctance to become concerned with cognition or consciousness in animals seems to result at least in part from a philosophical aversion rather than insurmountable barriers to scientific investigation. Perhaps because behavioral ecologists and ethologists feel more comfortable

dealing with evolutionary adaptiveness, they have seldom moved ahead to concern themselves with other equally significant aspects of animal life such as neurophysiological mechanisms or mental experiences.

## Definitions

It is helpful to begin by recognizing that conscious thinking is not a neat, homogeneous entity; for there are obviously many kinds and degrees of consciousness. Natsoulas (1978, 910–11) emphasized an important distinction that is often overlooked. One widespread meaning is what he designates as Consciousness 3, following the *Oxford English Dictionary*, “the state or faculty of being mentally conscious or aware of anything.” This Natsoulas calls “our most basic concept of consciousness, for it is implicated in all the other senses. One’s being conscious, whatever more it might mean, must include one’s being aware of something” (p. 910). Another important meaning is what Natsoulas calls Consciousness 4, as defined in the *OED*, “the recognition by the thinking subject of its own acts or affections.” Natsoulas adds to this definition of Consciousness 4: “One exemplifies Consciousness 4 by being aware of, or by being in a position to be aware of, one’s own perception, thought, or other occurrent mental episode” (p. 911). The other shades of meaning analyzed by Natsoulas (1983, 1985, 1986, 1988) are less important for our purposes although some of them might apply to non-human animals, but these two impinge directly on the issues discussed in this book.

Natsoulas’s Consciousness 3 is essentially conscious perception, and it can conveniently be termed perceptual consciousness. Its content may entail memories, anticipations, or thinking about nonexistent objects or events as well as immediate sensory input. An animal may think consciously about something, as opposed to being influenced by it or reacting to it without any conscious awareness of its existence or effects. Consciousness 4, as defined by Natsoulas, entails a conscious awareness that one is thinking or feeling in a certain way. This is conveniently called reflective consciousness, meaning that one has immediate awareness of one’s own thoughts as distinguished from the objects or activities about which one is thinking. The distinction between perceptual and reflective consciousness is crucial to the sometimes confused (and almost always confusing) debate among scientists about animal consciousness.

Many behavioral scientists and philosophers such as Lloyd (1989, 186) feel it is likely that animals may sometimes experience perceptual

consciousness, but that reflective consciousness is a unique human capability. This view is often expressed in the assertion that animals may know certain things, but they do not know that they know. This widespread view is shared even by those ethologists who are most inclined to ascribe conscious mental experiences to animals, for example, Crook (1983, 1987) and Cheney and Seyfarth (1990a). Many who doubt or deny that animals are conscious use the term to mean reflective consciousness. Reflective consciousness would be difficult to detect in animals, if it does occur. People can tell what they are thinking about, but animals are held to be incapable of doing so, although animal communication may often serve the same basic function, as discussed more fully in chapters 8 to 12. This very difficulty of detecting whether animals experience reflective consciousness should make us cautious about ruling it out. But most of the suggestive evidence that will be discussed in this book points towards perceptual rather than reflective consciousness, and those swayed by a visceral feeling that some important level of consciousness *must* be restricted to our species may cling to reflective consciousness as a bastion still defended by many against the increasing evidence that other animals share to a limited extent many of our mental abilities.

Reflective consciousness entails a simple form of introspection, that is, thinking about one's own thoughts. Introspection was once a very active and popular area of research in psychology, but was long ago abandoned under the influence of behaviorism. Even after the cognitive revolution, few if any psychologists have revived introspection as a method of studying the operation of mind or brain. It is therefore somewhat ironic that many behavioral scientists who resist assigning any significance to the notion of animal consciousness tend to fall back on introspection as a criterion of human uniqueness.

There is an intermediate category that is not clearly dealt with by Natsoulas's definitions. An animal might be consciously aware of some part of its own behavior—for example, of its act of eating food or fleeing from a predator. This would be a special case of perceptual consciousness. But such an animal might be incapable of thinking that it, itself, was eating or fleeing. If so, it would be capable of perceptual consciousness about its own behavior but not of reflective consciousness that it, itself, was the actor. Yet if we grant animals perceptual consciousness of their own actions, the prohibition against conscious awareness of who is eating or fleeing becomes a strained and artificial restriction. An animal capable of perceptual consciousness must often be aware that a particular companion is eating or fleeing, that is, it must be con-

sciously aware of both the action and of who is performing it. A perceptually conscious animal could scarcely be unaware of its own actions of eating or running away. Thus if we deny all reflective consciousness to such an animal, we are in effect proposing that its mental experiences entail a large "perceptual black hole" centered on its own activities. These considerations call into question the strong tendency of many scientists to hold that self-awareness is a unique human capability, as discussed in more detail in chapter 12.

Philosophers strive to clarify their own thinking and to help others do likewise. This leads them to refine and sharpen their definitions of important terms like thinking and consciousness. A few philosophers have focused their attention on the possibility that animals may experience some sorts of thoughts, and in doing so they have proposed a variety of definitions. But they do not all agree on such definitions, perhaps because of differing emphases on what seem to each philosopher to be the most important attributes of conscious thinking. The heterogeneity of human consciousness may explain the variety of philosophers' definitions, because they emphasize differing aspects of conscious experience. I have previously reviewed some of the more thoughtful and pertinent attempts to arrive at clear and useful definitions of mental terms (Griffin 1981, 1982, 1984, 1986). But behaviorists find almost any definition inadequate because it does not point the way to specific operational tests by which mental states can be identified.

These difficulties arise in large part because mental states appear to be processes rather than tangible entities. Something goes on in a central nervous system when someone desires, believes, remembers, anticipates, or decides. To the best of our very limited knowledge, these processes result from dynamic interactions between numerous excitations, inhibitions, and spontaneous or endogenous activity at synapses in the central nervous system. There is no reason to suppose that a specific neurohumor for desiring, believing, or deciding permeates the brain and produces these mental states, nor are there specific parts of the brain uniquely active during anticipation or choosing of particular actions. Many behaviorists argue that to postulate that conscious thinking affects behavior is to claim that a nonmaterial factor interacts with the physical world. But processes and relationships are in a sense immaterial, yet effective and important. Conscious thinking is in all probability an activity or attribute of central nervous systems, a functional process by which a brain supports mental activities of which the person or animal is consciously aware. Although mental experiences entail something more than information processing, as argued cogently by

Loewer (1987), this additional attribute need not be anything apart from the physical universe. A crude analogy is the distinction between the hardware and the software of computer systems; the latter is something different from the information-handling mechanisms, but not anything that is different in kind from other physical processes and relationships.

A major part of the perceived difficulty of providing a definition of conscious mental experience acceptable to scientists has been their insistence that such definitions must be based on objectively identifiable and observable properties. But consciousness is essentially a subjective attribute, as we know from personal experience. One of the most basic aspects of conscious thinking is the contemplation of objects and events, and one of the major challenges of cognitive ethology is to learn to what extent other species experience something similar. It need not be identical to human conscious experience; indeed, it is likely to differ substantially in accordance with the animal's way of life, its sensory capabilities, and its capacity for learning, memory, and anticipation. This strong desire for tangible, objective criteria may explain why many philosophers of mind refrain from proposing explicit definitions of the mental states with which they are concerned. But some attempts at definition are of interest because of the way that recently discovered facts about animal behavior can be related to them.

The materialist philosopher Armstrong (1981, 4–10) defined mental occurrences as states or processes in the central nervous system that are potentially capable of producing behavior, that is, he considered thoughts to be dispositions to behave in certain ways. This definition allowed him to escape from the serious limitation posed for the behaviorist's definition of thinking as verbal behavior by the obvious fact that we can think and feel without speaking or otherwise expressing our mental states. Armstrong defined consciousness as perception of one's own mental states—a definition close to Natsoulas's Consciousness 4, or what I have been calling reflective consciousness. Another materialist philosopher, Bunge (1980), begins his book about the nature of minds by stating that "perceiving, feeling, remembering, imagining, willing, and thinking are usually said to be mental states or processes. (We shall ignore . . . the quaint view that there are no such facts)." Bunge claims that an ability to learn is necessary for mental states, and that such plasticity is confined to birds and mammals; but he overlooks extensive evidence of learning in a wide variety of vertebrate and invertebrate animals.

Half a century ago, when symbolic communication in animals was



unknown and generally believed to be impossible, Price (1938) conceded that if animals did use symbols we would have to assume that they have minds. And in a series of Gifford Lectures at Edinburgh, *The Development of Mind*, the philosopher Kenny (1973, 47) stated that “to have a mind is to have the capacity to acquire the ability to operate with symbols in such a way that it is one’s own activity that makes them symbols and confers meaning on them.” In emphasizing the importance of symbolic communication as a criterion of mind, Kenny continues: “The pursuit of self-selected goals that go beyond the immediate environment in space and time is not possible without the use of symbols for the distant, the remote, and the universal. And on the other hand, the use of symbols itself involves purposes which go beyond the temporal and spatial present.”

The examples of animal communication discussed below in chapters 8 to 11 satisfy Kenny’s criterion in a general way, but symbolic communication is especially evident in the dances of honeybees described in chapter 9. For it is certainly the bee’s own activity that makes her waggle dance a symbolic statement. The dances of scouts from a swarm of bees that have visited cavities report their distance, direction, and desirability to their sisters in a situation where the symbolic communication is well removed in space and time from the objects it describes. Although the separation in time is ordinarily only a few minutes, in special situations waggle dances refer to a cavity or a food source that the dancer has not visited for several hours (von Frisch 1967, 350).

Some may object that we can voluntarily coin new words, or at least select our symbols and thus endow them with meaning, while the goals of dancing bees may be assumed not to be self-selected but to be automatic results of hunger or other internal physiological states. These in turn are often assumed to set off genetically programmed behavior patterns that are held not to be accompanied by conscious thinking. But, as discussed in chapter 12, the customary equation of instinctive with unconscious rests on a very flimsy basis. The denial that the honeybee communication system is truly symbolic amounts to an a priori denial that bees are conscious, which denial is then used to justify the rejection of their communication as symbolic. In other words the definition of symbolic comes to have an unstated requirement of conscious selection of signals along with an implicit assumption that this is something of which insects are incapable.

Baars (1988) suggests the following definition of consciousness from the viewpoint of a cognitive psychologist: “We will consider

people to be conscious of an event if (1) they can say immediately afterwards that they were conscious of it *and* (2) we can independently verify the accuracy of their report." Many of the examples of animal communication discussed in chapters 8 to 12 satisfy this requirement, since the animal communicates some simple statement about what it is doing, and we can readily verify the accuracy of the statement. If one requires that true consciousness must be reflective, that is, Natsoulas's Consciousness 4, the communication that there is a dangerous predator approaching would fail to demonstrate such true consciousness unless it included something equivalent to "I am conscious that a dangerous predator is approaching."

The physicist Longuet-Higgins (1972, 136) in the same series of Gifford lectures suggested that "the idea of a goal is an integral part of the concept of mind; and so is the idea of 'intention'. An organism which can have intentions I think is one which could be said to possess a mind. . . . The concept of intention . . . involves the idea of the ability to form a plan, and make a decision—to adopt the plan. The idea of forming a plan, in turn, requires the idea of forming an internal model of the world." Philosophical ideas about the importance of intentions in communication have been thoroughly reviewed in the book edited by Cohen, Morgan, and Pollack (1990). Most of these philosophers take for granted that human intentions are ordinarily conscious plans to do something in the future, but the possibility of nonhuman intentions is scarcely mentioned in such philosophical discussions.

Yet animals certainly seem to form at least simple plans and make decisions about what actions are likely to achieve what they want. Much of their learned behavior is necessarily based on some sort of acquired representation that models some important aspect of the external world. Although anticipation and planning are impossible to observe directly in another person or animal, indications of their presence are often observable. Early ethologists such as Heinroth, and especially Lorenz in the 1930s, studied the intention movements of birds (reviewed by Lorenz 1971) and pointed out that these small-scale preliminaries to major actions such as flying often serve as signals to other animals. Although Lorenz interpreted intention movements as indications that the bird was planning and preparing to fly, the term "intention movement" has been quietly dropped from ethology in recent years, presumably because behaviorists feared that the term had mentalistic implications. On the other hand, some modern ethologists recognize that animals do have at least simple intentions (Krebs and Dawkins, 1984; Guilford and

Dawkins, 1991), although they avoid describing such intentions as conscious.

Daanje (1951) described a wide variety of intention movements in many kinds of animals, but his primary interest was in the tendency of such movements to become specialized communication signals in the course of behavioral evolution. The possibility that intention movements indicate the animal's conscious intention has been neglected by ethologists during their behavioristic phase, but we may hope that the revival of interest in animal thinking will lead cognitive ethologists to reopen the study of the degree to which intention movements may indeed be signals of conscious intent. The very fact that they so often seem to evolve into communicative signals may reflect a close linkage between conscious thinking and its communicative expression.

Later chapters will describe several suggestive examples, such as beavers piling material around sturdy fencing protecting a tree with the apparent intention of reaching the unprotected trunk and branches, which they then cut; cooperative hunting by lionesses; and honeyguides calling and leading human honey gatherers to distant bee nests. In all these and many other cases it is difficult to deny that the animals form and execute simple plans. But the dance communication of honeybees discussed in chapter 9 provides us with one of the best windows through which we can discern signs of intentional planning. The scouts that have found very desirable cavities seem to be urging their sisters to go there, and according to Lindauer (1955, 1971) this urging can be altered by following dances of other bees describing better cavities. Furthermore, a decision of great importance to the bees is reached on the basis of long series of communicative exchanges of information about different cavities. These are only a few examples of animal behavior that satisfy Longuet-Higgins's criterion of mind.

Millikan (1984, 1989) doubts that bees and birds "have inner representations in the same sense that we do." This wording exemplifies a recent trend to shift from denying that animals experience any significant thoughts to a more modest claim that their thoughts are different from ours. Millikan goes on to list several ways in which she believes that the internal representations of nonhuman animals differ from human beliefs. But many of these features do appear to be present in the memories and decision-making processes exhibited by animals. For example, she claims that only members of our species can "combine beliefs with beliefs to yield new beliefs." But it seems likely, for example, that when an animal believes that a predator is threatening and also believes

that its burrow is nearby, its resultant dash to the familiar shelter results from combining these two beliefs into a belief that it should rush to the burrow. Another distinguishing feature proposed by Millikan is that animal signaling does not seem to her to involve a separation of indicative from imperative functions of internal representations, whereas she emphasizes that "human beliefs are not tied directly to actions." But certainly many, perhaps most, of our beliefs are related to actions of some sort. And insofar as animals may entertain beliefs that are not related to any observable behavior, we would have difficulty gathering evidence of their occurrence.

### Significant Ideas about Animal Consciousness

The nature of consciousness and the extent to which it occurs are major and basic problems of psychology and the philosophy of mind. In addition to the penetrating analyses of major philosophers of previous centuries, some contemporary psychologists and philosophers have rejected the dogmatic pessimism that characterizes many behavioral scientists; and they have discussed the possibility that some animals do experience conscious thoughts. For instance, Dunbar (1988) finds it likely that higher vertebrates at least "themselves do a great deal of their cost-benefit processing on a cognitive plane." Armstrong-Buck (1989) has reviewed recent developments in the study of animal cognition from the perspective of Whitehead's philosophy. The "biophilosopher" Rensch (1971, 1985) recognized the likelihood that simple sorts of conscious experience occur in a wide variety of animals, and so do the authors of several chapters in the recent books edited by Bekoff and Jamieson (1990) together with other philosophers whose views are discussed in chapter 12.

To be sure, some philosophers "reject the concept of consciousness as otiose in the study of animal knowledge," in the words of Heyes (1987), who argues that cognitive ethology is beset by muddled thinking. Dore and Kirouac (1987) argue that cognitive ethology is misguided because it depends on inadequate definitions. Yoerg and Kamil (1991) object strongly to any ascription of conscious experiences to animals, and urge that cognitive ethology restrict itself to an analysis of cognition that is assumed to be unconscious. Dickinson (1980, 5) saw "no reason why mental processes should not be inferred from behaviour"; but more recently he has argued that "manifest intentionality of behaviour" is not sufficient to demonstrate mental states (Dickinson

1988, 323). Most of the authors in the collection of papers edited by Davey (1983) are reluctant to credit nonhuman animals with significant mental states. And Dennett (1989) has asserted, without qualification or justification, that the attempt to study animal consciousness is a wild goose chase or, at least, impossibly difficult (Dennett 1991, 446).

Mackintosh (1987) concludes that rats know about the consequences of their actions, but feels that "this is not necessarily an appropriate language for scientific analysis," thus expressing the intellectual conflict experienced by many contemporary students of animal behavior. Recent symposia edited by Hoage and Goldman (1986) and by Jerison and Jerison (1986) discuss animal intelligence from a variety of viewpoints; and although the traditional inhibitions generally prevail, the authors of some chapters edge closer than usual to considering animal consciousness. Two books published in the 1980s exemplify this trend. The first, by a psychologist, concludes: "Our organ of thought may be superior, and we may play it better, but it is surely vain to believe that other possessors of similar instruments leave them quite untouched" (Walker 1983, 388). The second, by two philosophers, emphasizes that "in dismissing consciousness as superfluous, one sets limits on one's explanatory apparatus. It is important to realize that the limits are set by choice, self-imposed, not dictated by any fundamental principles of scientific methodology. There is room for consciousness if one is willing to make room for it" (Radner and Radner 1989, 208).

Later chapters will explore what we can find in the extensive data on animal behavior when we do make room for animal consciousness. My approach will entail tentatively considering animals as conscious, mindful creatures with their own points of view; and I will attempt to infer, as far as the available evidence permits, what it is like to *be* an animal of a particular species under various conditions. As emphasized by Dretske (1988), it is important to distinguish between what animals *do* and what happens to them; it seems likely that a considerable amount of animal behavior results from an animal's doing something rather than being a passive object that is simply affected by the world around it. This review of the published literature is by no means exhaustive. I have selected cases where versatile behavior patterns and apparently intentional communication are reasonably well understood, but many other examples are equally suggestive. I will emphasize wild animals living under reasonably natural conditions, not because pets, domestic animals, and wild animals in captivity do not show equivalent evidence of conscious thinking, but simply because an adequate review of the rele-

vant evidence concerning domestic animals would require another whole book.

To any biologist it will be almost self-evident that insofar as animals do experience conscious thoughts or subjective feelings, these will not be unitary all-or-nothing phenomena. Certainly our own thoughts and feelings vary enormously in their nature and complexity and in the relative importance of conscious and unconscious processes, as emphasized by Shallice (1978, 1988a, 1988b). But before we can hope to analyze how the content and quality of consciousness varies from species to species and from one situation to another, we must determine where and when it occurs. The relatively simple content of animal thoughts and subjective feelings is almost certainly relevant to the animal's own situation rather than to human concerns. This makes the quest for evidence of consciousness more difficult than if we were searching for a single, well-defined entity comparable, say, to color vision. But the lack of simplicity does not render something unimportant or impossible to detect, analyze, and understand.

### Objections of "Inclusive Behaviorists"

Many people find it difficult to understand why so many behavioral scientists are adamantly reluctant to consider animal consciousness. The historical reasons, thoroughly reviewed by Boakes (1984), Burghardt (1973, 1978, 1985a, 1985b), Dewsbury (1984), and Rollin (1989, 1990), have involved a reaction against excessively generous interpretations of isolated instances of animal behavior that suggested rational thinking and insight. Coupled with this rejection of mentalism was an equally fervent rejection of the idea that genetic influences as opposed to individual experiences had a significant effect on human or animal behavior. Although genetic control of behavior is logically a wholly different matter from the significance of subjective mental experiences, the two issues have tended to be linked in theoretical consideration of animal behavior and mentality, as discussed by Burghardt (1978). In psychology these distinct but closely coupled trends were combined in behaviorism, as advocated most influentially by Watson (1929) and Skinner (1974). During the same period a strong reductionist tradition also developed in biology, typified by the views of Loeb (1912), who, although he believed in the existence of human consciousness, argued that all animal and even much human behavior could be explained in terms of tropisms. In their zeal for objective proof of any claims about

animal behavior or mentality, most of the psychologists who established the long dominant behaviorist movement insisted on three major points:

- I. Learning and individual experience account for almost all behavior not directly controlled by the animal's structural capabilities.
- II. Only external influences and directly observable behavior should be considered in explaining what animals (or people) do; behavioral scientists should limit their concern to observable inputs to and outputs from the black box called an organism. And
- III. Subjective mental experiences, especially conscious thinking, should be ignored for two reasons:
  - A. They are unmeasurable "private" phenomena, perceptible only by the one who experiences them, so that statements about them cannot be independently verified, and
  - B. They have no influence on behavior, and are thus incidental byproducts of brain function, or epiphenomena.

Claim I of behaviorism has been largely abandoned, although it used to be vigorously defended by many behavioral scientists who reacted against any suggestion that behavior might be genetically influenced with much the same fervor as that currently directed against suggestions that mental experiences may occur in animals and exert some influence on their behavior. Extensive evidence shows that what animals learn is strongly constrained by species-specific capabilities; some behavior patterns are learned much more easily than others that the animal is quite capable of performing. Furthermore, the widespread interest in socio-biology has led to a strong emphasis on the adaptive value of behavior—how it increases the likelihood of an animal's survival and reproduction and, hence, its evolutionary fitness.

Claim II has also been greatly modified due to the cognitive revolution in psychology. As summarized by Roitblat, Bever, and Terrace (1984, 1):

Animal cognition is concerned with explaining animal behavior on the basis of cognitive states and processes, as well as on the basis of observable variables such as stimuli and responses. For a time it appeared, at least to some, that discussion of cognitive states was not necessary, either because they were exhaustively determined by environmental events, or because they were epiphenomenal and without any causal force. In any case, it was assumed that a sufficiently detailed description of overt events would suffice for explanation. A great deal of the research into animal behavior has made it clear, however, that

such cognitive states are real and necessary components of any adequate theory that seeks to explain animal behavior.

These cognitive states "include learning, remembering, problem solving, rule and concept formation, perception, (and) recognition" (Roitblat 1987, 2).

Animal cognition has thus come to be accepted as real and significant, and its investigation is recognized as important, as reviewed in the volume edited by Ristau (1991). Menzel and Wyers (1981) and Menzel (1991) consider that the foraging behavior of animals entails cognition, and Wyers (1985) concludes that cognitive concepts are useful in analyzing the behavior of sticklebacks. But animal consciousness is still taboo, both among biologists who study animal behavior and psychologists such as Terrace (1984, 7), who asserts that "both in animal and human cognition it is assumed that the normal state of affairs is unconscious activity and thought."

Although biologists have always tended to dissent from claim I of behaviorism, they have generally concurred with psychologists in accepting claims II and III. Therefore it will be convenient to refer to both groups collectively as "inclusive behaviorists." Despite renewed interest in animal cognition, the scientists who are willing to venture into this difficult area have tended to cling tightly to the security blanket of conventional reductionism. Although most philosophers have long since abandoned logical positivism, and cognitive psychologists now reject the negative dogmatism of the strict behaviorists, students of animal behavior are still severely constrained by a guilty feeling that it is unscientific to inquire about subjective feelings and conscious thoughts (Colgan 1989; Heyes 1987; Latto 1986; Snowdon 1991; and Yoerg and Kamil 1991). Although ethologists have recognized more and more complexity and versatility in animal behavior, many have lagged behind the cognitive psychologists and continue to try dutifully to fit all the new knowledge about animal behavior into the same old pigeonholes that seemed sufficient years ago to Pavlov and Watson. Thus the ghost of Jacques Loeb (1918) still makes its cold and clammy influence felt when animal behavior is described solely in terms of stimuli, responses, and adaptive advantages.

Aside from Lorenz (1971) and Hediger (1947, 1968, 1976, 1980), very few ethologists have discussed animal thoughts and feelings in recent years. While seldom denying their existence dogmatically, they emphasize that it is extremely difficult, perhaps impossible, to learn anything at all about the subjective experiences of another species. But the



difficulties do not justify a refusal to face up to the issue. As Savory (1959, 78) put the matter, "Of course to interpret the thoughts, or their equivalent, which determine an animal's behaviour is difficult, but this is no reason for not making the attempt to do so. If it were not difficult, there would be very little interest in the study of animal behaviour, and very few books about it."

It is often claimed that human language is what makes conscious thinking possible for us, but that no other species has this capability, as argued by Adler (1967) and Davidson (1982, 1984). This view is widely held even by those who believe it probable that some animals experience at least perceptual consciousness (Natsoulas's *Consciousness* 3). For example, Rensch (1971) distinguished human from animal consciousness on the ground that the former but not the latter is normally expressed verbally. But increasing understanding of the versatility of animal communication makes the distinction between animal communication and human language a less crucial criterion of human uniqueness.

As pointed out by the philosopher Karl Popper (1978), what he termed "mental powers" are presumably helpful to animals in coping with the challenges they face, and therefore must contribute to their evolutionary fitness. He emphasized how useful it is to think about alternative actions and their likely consequences before they are actually performed. This of course serves to replace trial and error in the real world, where error may be costly or fatal, with decisions based on thinking about what one may do. Popper seemed to imply that such mental trial and error is a uniquely human capability, but the versatility of much animal behavior suggests that on a very simple and elementary level they sometimes think about possible actions and choose those they believe will lead to desired results or avoid unpleasant ones.

Scientists often insist that any significant hypothesis must be falsifiable, which means that we must be able to anticipate how it might be confirmed or disconfirmed, even if the necessary procedures are not immediately practicable. Scientists lose interest in a theory if no one can suggest how to ascertain whether it is correct or not. Thus it was not entirely unreasonable for Percival Lowell to postulate that there were canals on Mars, given the limited data available to him. This was clearly a testable hypothesis, and Lowell or his contemporaries could readily imagine that future astronomers using improved telescopes or spacecraft might determine whether there were canals or not. As we now know, when suitable pictures of the Martian surface became available, they disconfirmed Lowell's hypothesis, although riverlike erosion pat-

terns, too small to be resolved by terrestrial telescopes, do indicate that there was once liquid water on Mars. Some strict behaviorists object to all hypotheses about conscious experiences in animals, or even in people, on the ground that they cannot imagine any procedure by which such hypotheses can be confirmed or falsified. This may tell us something about the limited imaginations of scientists, and outside of narrow scientific circles this argument is no more convincing than that of the solipsist philosopher who insists that he is the only conscious person in the universe. At early stages in the development of any branch of science it is often necessary to do the best one can with fragmentary evidence and hypotheses that cannot be neatly formulated into crisp alternatives for the very reason that the subject is poorly understood.

### Limitations of the Objections

To claim that it is impossible to study subjective experience scientifically is to overlook the fact that many scientific advances have begun by exploratory probes into unknown areas where clearcut evidence is not initially available. For example, Darwin and Wallace could not directly observe and measure the evolution of animals or plants in the remote past. Had they been inhibited from speculative inferences by the sort of paralytic perfectionism that prevents inclusive behaviorists from investigating animal consciousness, one of the most far-reaching of scientific developments would have been severely hampered if not prevented altogether.

It is not correct to argue, as some have done, that even considering animal consciousness entails a lowering of scientific standards. This argument confuses critical standards with narrow-mindedness. Inquiring about unknown or neglected subjects calls for questioning and exploring possible approaches, what is sometimes called pre-science. When such explorations lead to suggestions and hypotheses, these should of course be scrutinized and evaluated with the highest critical standards. But to rule out a plausible possibility as unscientific is a sort of self-imposed handicap or even blindness. In the words of Kety (1960, 1862) "Nature is an elusive quarry, and it is foolhardy to pursue her with one eye closed and one foot hobbled."

Equally mistaken is the charge that to suggest animals may sometimes be conscious smacks of postulating immaterial or supernatural entities. Conscious thoughts and subjective feelings are generally agreed to result from activities of central nervous systems, and there is no reason to doubt that these are governed by the principles of natural science.

Taking it for granted that consciousness exists in at least one species, it is a valid and significant question to ask to what extent it also occurs in others. A related confusion is the implication that to suggest animals may consciously plan what to do in the immediate future is somehow akin to postulating a divine purpose causing the diversity of animals and the complexity of their structure. A moment's thought should suffice to dispel this lingering vestige of the nineteenth-century debates about divine creation versus evolution influenced by natural selection.

### Anthropomorphic Objection, and Conceit

For many years any consideration of animal consciousness was strongly discouraged by the accusation that it was anthropomorphic. This widespread attitude resulted from the recognition that many earlier ascriptions of human thoughts to animals were wholly unjustified. But the charge of anthropomorphism had been inflated to include even the most tentative inference of the simplest kind of conscious thoughts by animals. We were, in effect, brainwashed into equating the belief that a horse could carry out long division with the suggestion that a rabbit consciously anticipates escaping from a fox by plunging down its burrow. When one carefully examines such charges of anthropomorphism, it turns out that they entail the implicit assumption that whatever it is suggested the animal might do, or think, really *is* a uniquely human attribute. Such an assumption begs the question being asked because it presupposes a negative answer and is thus literally a confession of pre-judgment or prejudice. This point has been emphasized by Bennett (1964, 11), Burghardt (1973, 1985b, 1991) and especially by Fisher (1987, 1990) who has spelled out in considerable detail why there is no basic, philosophical basis for the taboo against anthropomorphism as it has been perceived by most scientists. When applied to the suggestion that animals might think about simple things that are clearly important to them, this charge of anthropomorphism is a conceited claim that only our species is capable of even the simplest conscious thinking.

### The Inverse "Clever Hans Error"

Students interested in animal behavior have long been haunted by the specter of "Clever Hans errors." Suggestions that an animal might be consciously aware of the likely results of its behavior routinely elicit a sort of knee-jerk reflex accusation that they result from Clever Hans errors (Sebeok and Rosenthal, 1981). This hazard refers to the apparently

intelligent performance of a trained horse named Hans, whose devoted trainer believed he could add, subtract, multiply, and even divide written numbers. Hans gave his answers by tapping with his forefoot, eight taps when  $2 \times 4$  was displayed, twenty-seven taps in response to  $3 \times 9$ , and so forth. Some skeptics were troubled by the fact that Hans solved difficult arithmetical problems about as rapidly and apparently as easily as simple ones (Washburn 1917). But he tapped correct answers even when others beside his familiar trainer presented the problems, and many scientists were convinced that he understood the problems and arrived at correct answers by a sort of mental arithmetic.

A psychologist, Oskar Pfungst, showed by careful experiments that Hans was not watching the written numbers but the person who presented the problem. If no one was visible, or if the person did not know the correct answer, Hans tapped his foot at random. What Hans had actually learned was to detect the small and inadvertent motions that people made while watching to see whether he stopped after the correct number of foot taps. Even when observers tried to avoid doing so they could not help revealing by subtle motions or facial expression when the right number of taps had been produced. In his detailed account of these experiments Pfungst (1911) described many other complex patterns of behavior learned by Hans and showed that they all depended on inadvertent cues from human companions.

The saga of Clever Hans has been almost universally accepted by scientists as a definitive example of mistaken inference of complex mental abilities in animals. But this enthusiastic application of scientific caution has mushroomed into denial that animals experience even the simplest conscious thoughts. Inability to do arithmetic has been taken as evidence for the absence of any thinking whatever. What has been almost totally overlooked is the real possibility that Clever Hans was consciously thinking something simple but directly relevant to his situation—perhaps something like: “I must tap my foot when that man nods his head.” The horse’s behavior was quite consistent with such an interpretation, but scientists’ enthusiasm for debunking unjustified inferences has trapped them for generations into a dogmatic dismissal of the plausible alternative that animals may experience simple conscious thoughts, even though quite incapable of mental arithmetic.

The perceptual discrimination needed to detect inadvertent counting gestures has been recognized as remarkable and significant. Many animals are known to have sensory abilities exceeding or differing from our own. Dogs can smell differences between clothing worn by different people, insects discriminate the plane of polarization of light, bats and

other small mammals hear frequencies far above the human range, and sharks are so sensitive to electric currents that they can detect buried prey by the electrical potentials from their heartbeats. But such “super-human” sensory capacities are simply different input channels to the central nervous system, and their refinements tell us little or nothing about any subjective thoughts that the animal may experience.

The detailed observations by ethologists under natural conditions, reviewed in chapter 3, have shown that many animals monitor the behavior of predators and react to very slight changes in posture or behavior that signal a likelihood to attack. Predators are also very adept at noticing the slightest indications that potential prey are weak or sick, which make them easier to capture. The same basic neurophysiological mechanisms that underlie such finely tuned discriminations under natural conditions are probably employed by trained animals when they learn to respond to inadvertent counting movements of their human trainers.

### Discredit by Exaggeration

Scientists often dismiss suggestions of animal consciousness by overinterpreting them to include complex levels of thinking that are clearly beyond the capabilities of nonhuman animals. This attitude was recently parodied on the cover of an issue of Newsweek which included a balanced review of the current revival of interest in animal thinking and intelligence. But the cover picture shows a dog with a balloon rising from his head, and in the balloon the formula  $e = mc^2$ . This is a typical exaggeration of the suggestion that animals may think about simple matters that are important to them into an implication that they share the more complex levels of human thought. Another example of this tendency to exaggerate that which one wishes to deny is provided by Ingold's (1988) implication that those who suggest animals may sometimes think consciously are claiming that *all* nonhuman animals *always* do so, as discussed below in chapter 4.

It is important to recognize that we all make useful, and generally correct, inferences about the conscious thoughts of other people by observing their behavior, especially their communicative behavior. The same basic approach is equally applicable to animal minds. When animals communicate, as they often do, they may sometimes be expressing conscious thoughts. Many animals exchange rich repertoires of communicative signals, especially those that serve to regulate their social behavior. Indeed, mental experiences may constitute the primary con-

tent of communicative signals, both human and animal. To the extent that communicative signals convey conscious thoughts and subjective feelings, they can be used as objective, independently verifiable evidence about the mental experiences of the animals themselves.

Additional indications of animal consciousness arise from the versatility with which they sometimes cope with novel and unpredictable challenges in simple but apparently rational ways. While it is impossible to prove with totally logical rigor that an animal thinks consciously about what it is doing, even when it behaves intelligently, behavioral versatility does provide suggestive evidence that is too significant to ignore—though behavioral scientists have customarily done so.

### Reasons to Infer Animal Consciousness

Out of all these multiple crosscurrents of ideas, three categories of evidence stand out as the most promising sources of significant, though incomplete, evidence of conscious thinking by nonhuman animals. They will be reviewed in the following chapters:

- I. Versatile adaptability of behavior to novel challenges (discussed in chapters 2 to 6);
- II. Physiological signals from the brain that may be correlated with conscious thinking (discussed in chapter 7);
- III. Most promising of all, data concerning communicative behavior by which animals sometimes appear to convey to others at least some of their thoughts (discussed in chapters 8 to 11).

Finally, after all this suggestive evidence has been reviewed, it will be appropriate to consider (in chapter 12) several general questions that are relevant to the question of animal mentality.

## *Finding Food*

**L**ocating suitable food is one of the most widespread and pressing problems faced by animals. Unlike pets and laboratory animals, most wild animals must spend a large fraction of their waking hours locating food and extracting it from their environments. In the case of herbivores, this may seem simple at first thought; but it is seldom an easy matter of wandering about nibbling whatever vegetation is encountered. Not all plants are equally nutritious by any means, and even grazing animals that appear to need nothing but abundant grass do pick and choose just which patches are most worth cropping. Many herbivores must pay considerable attention to signs that food is available from particular plants, and the tactics they employ often call for at least simple levels of learning and perhaps conscious thinking. Active predators face more obvious challenges because they must not only locate but also pursue and capture prey animals that seldom wait passively to be eaten but devote considerable effort, and sometimes thought, to avoiding that fate.

Foraging behavior varies widely, and its versatility is not closely correlated with the phylogenetic group to which the animals belong; so-called lower animals often display ingenuity comparable to that of mammals. This review of feeding tactics that suggest thinking on the animal's part will be divided rather arbitrarily into categories that can be roughly characterized as feeding on passive and active prey. This chapter will be devoted to the former category, in which the food consists of plants or of animals that are relatively inactive, so that the principal problems are how to locate food and handle it. Chapter 3 will concentrate on predation upon prey that exert effective efforts to escape and can be taken only by means of actively versatile tactics. In some significant situations these tactics include coordinated action by two or more individual predators, and such cases are often very suggestive of simple conscious thinking on the part of the cooperating animals.

## Foraging Decisions by Bumblebees

Bumblebees would not seem likely to employ a high order of thoughtful decision making, but when Pyke (1979) analyzed in detail the ways in which a particular species of bumblebee (*Bombus appositus*) gathered nectar from clusters of monkshood flowers in the Colorado mountains, he found that they followed fairly complex rules. These flowers vary considerably in nectar content, depending in part on whether an insect has already removed nectar from a particular flower. Pyke marked bumblebees so that individuals could be distinguished, and recorded their behavior when visiting clusters of flowers that had not been visited by other insects. No one flower held enough to fill a bumblebee's stomach, so that several had to be visited before she flew off to her nest. The flower closest to the ground, or the next to lowest, was almost always visited first, and the bumblebee then moved upward, usually selecting the closest flower she had not already visited. Out of 482 observations, the same flower was visited twice on only five occasions. Either the bumblebee remembered for a short time which flower she had already visited, or else she left a scent mark or some other indication that enabled her to avoid wasting her time on empty flowers.

The simplest rules that Pyke (1979, 1170) could formulate to account for the foraging tactics of these bumblebees took the following form: "Start at the lowest flower on a given inflorescence, then move to the closest flower not already visited, unless the last movement had been downward and was not in fact the first switch from one flower to another on a particular inflorescence. In the latter case, move to the closest higher flower not just visited." The formulation of these rules in English may make them seem more complicated than they actually are, but even if simplified into a set of actions within the capabilities of a foraging bumblebee, they are not the simple, stereotyped sort of reactions we are accustomed to expect from insects.

Many other insects engage in equally ingenious foraging behavior, but most are difficult to study because they rely so heavily on olfaction, and because it is extraordinarily difficult to monitor and experimentally manipulate the chemical signals that guide their behavior. Locating food may entail searching for the odors that signal its availability, following gradients in the concentration of such odors, or simply moving upwind when they are detected. In other cases where insects use vision to locate food sources, as when bees and other insects that feed on pollen and nectar search for flowers, they are so small and move so rapidly that it is very difficult to determine just what searching movements they



employ. But I suspect that when cognitive ethnologists become sufficiently disinhibited from the mindset that views all insects as genetically programmed clockwork, they will devise effective methods to monitor how insects go about searching for food. This in turn might disclose that many species are at least as versatile as the bumblebees studied by Pyke.

### Prey Selection by Starlings and Wagtails

Birds rely primarily on vision to locate and capture food, and they are easier to observe than many other animals. As a result, we know more about their behavior in general, and their foraging in particular. In some cases they are obliged to make choices in their search for food that would seem likely to be facilitated by a little simple thinking about the possibilities available to them and the probable results of various alternative courses of action. For example, a thorough study of a group of starlings in the Netherlands by J. M. Tinbergen (1981) revealed that when feeding nestlings, they concentrated primarily on two species of caterpillars, which were to be found in opposite directions from their nests. This made it possible to tell from their initial flight direction which of the two kinds of caterpillar they intended to gather. One of the two species was preferred under most conditions, but the parents switched to the other when there was a pressing need for food, and especially when their broods were experimentally increased by placing additional nestlings in their nest. These choices were made at or near the nest, where neither type of caterpillar was visible; the starlings had to remember in which direction to fly for each type.

A clear and reasonably representative example of the choices and decisions involved in feeding behavior stems from the studies of two species of wagtails feeding on Port Meadows along the banks of the Isis River in Oxford (Davies, 1977; Krebs and Davies, 1978). The pied wagtail (*Motacilla alba yarrellii*) is a year-round resident of southern England, and the yellow wagtail (*M. flava flavissima*) is a migrant present only during the summer months. They were studied early in the spring before they started to breed. At this time they were gathering food only for themselves, but were probably also putting on weight in preparation for the nesting season that would follow in a few weeks. They were easily observed because the grass was heavily grazed by cattle and horses, and the numerous dung pats provided food for the flies on which the wagtails fed. Only one bird at a time fed on insects from a single dung pat, but small groups often hunted at the pools where sev-

eral kinds of aquatic insects were abundant. At a particular dung pat the wagtail would usually capture only one of the larger flies, and this disturbance would cause the others to scatter into the grass. The bird would then search for and catch many flies in the immediate vicinity.

At the start of a feeding session each bird had to decide where to search for food, whether to join a flock of wagtails or hunt by itself, and whether to concentrate on dung pats or on aquatic insects at the shallow pools of water on low-lying areas. The wagtails made their choices with considerable efficiency, so that they obtained approximately the maximum possible amount of food with minimum expenditure of time and effort. This entailed concentrating their efforts where food was most plentiful and moving on when it became depleted. But these shifts were not rigidly programmed; they did not wait until every last fly had been captured, but moved to richer sources when the effort required to catch another fly became greater than that needed to move on. The shifts were not random; the wagtails moved to other areas where insects were plentiful. These decisions seemed to be based on seeing the larger flies on fresh dung pats. But the birds may well have also been influenced by memories of locations where they had found plentiful food in the recent past.

Behavioral ecologists who analyze feeding tactics such as those of the Oxford wagtails ordinarily avoid speculating about any possible thinking on the bird's part as it makes these decisions, which are important for its survival and reproduction. But the multiple factors that must be evaluated, and the unpredictable details of the feeding situations, would seem to render a little simple thinking helpful and therefore adaptive.

### Blackbirds' Decisions about Feeding Ecology

A detailed study of the behavioral ecology of marsh-nesting blackbirds by Orians (1980) has revealed how many subtle factors influence both the selection of insect prey and the choice of mates and nesting territories. The redwinged blackbird (*Agelaius phoeniceus*) and the somewhat larger yellowheaded blackbird (*Xanthocephalus xanthocephalus*) are abundant breeding birds in the marshes of northwestern United States and western Canada, and they nest in sufficiently open areas that most of their feeding behavior can be observed relatively easily. Orians and his colleagues concentrated on the nesting season when the parents are under great pressure to obtain enough food for their nestlings. This of course is a situation where natural selection operates powerfully on the birds' behavior; for the number of healthy young that can be raised de-

pend directly on the amount and quality of food their parents capture and bring back to the nest.

Both species of blackbirds nest in vegetation growing in shallow water. The redwing is strongly territorial; in the spring the males arrive first and establish territories that include an area of marsh or adjacent upland. Up to a dozen females arrive later, and, after visiting several male territories, each female settles in one, mates with the territorial male, and builds her nest within his territory. The females do all the nest building, incubation of the eggs, and almost all the feeding of the nestlings, although after the young have left the nest the males also feed them. The yellowhead males do help feed their nestlings, but otherwise the habits of the two species are similar. Both feed heavily on adults of aquatic insects that have just emerged from the water, but the redwings also feed on insects they find on the dry upland areas. The larger yellowheads exclude redwings from both their nesting territories and from the richest sources of aquatic insects.

Marshes vary greatly in the abundance of the insects on which the blackbirds feed, and the density of nesting birds is roughly correlated with insect abundance, although other factors also play a role. For example, the yellowheaded blackbirds avoid areas with a continuous stand of trees extending more than about 30 degrees above the horizon or, in one case, a marsh where tall cliffs rose abruptly from the water's edge. The tendency to avoid nesting in such areas, even when insect food is abundant, is probably related to the danger that hawks may select such trees for their nests.

It is important to recognize that the male blackbirds make extremely important choices about nesting territories well before their young hatch and require an abundant source of insect food. At this time very few aquatic insects have emerged, so that the choice of a territory must be guided by something other than the contemporary abundance of insects. Somehow they do ordinarily make appropriate choices, selecting out of extensive areas of marsh those localities that later produce the richest harvest of aquatic and terrestrial insects. One might suppose that these choices are guided by memory and tradition, the blackbirds simply remembering where they nested last year or where their parents raised them. But these marshes change rapidly from year to year due to ecological changes—such as variation in water level and invasion of lakes by carp—that drastically reduce the populations of aquatic insects. It seems that they must have some mental representation of a future situation.

Newly arrived blackbirds often forage at the air-water interface when

they are selecting territories. When the females arrive they seem to ignore the vigorous displays of the males and instead spend a great deal of time at the edge of the water. Perhaps they are looking for the aquatic larvae and nymphs of insects that will later emerge as adults, but Orians (1980) interprets his observations more conservatively in terms of vegetation patterns that indicate where aquatic insects are most likely to emerge as adult forms. Few insect larvae occur where the stalks of aquatic plants are closely spaced, but many can be expected to emerge at the outer edges of such areas. Female blackbirds may be looking for signs of future food sources as they decide where to settle and build their nests.

Behavioral ecologists tend to assume that some genetically determined action pattern guides these choices. They seldom allow themselves to speculate about any possible thoughts of blackbirds that examine several marshy areas, and choose one only after devoting a considerable amount of time. Might the birds think that certain types of marshy vegetation are more likely than others to provide abundant insects a few weeks later? While we have at present no way to answer such a question, it is important to realize that it remains open and that future investigations might provide at least a provisional answer.

For example, it might turn out after appropriate investigation that part of the male's display behavior communicates to females some such message as "Lots of insects here." How could ethologists hope to test this hypothesis? Experimental procedures have been developed that indicate which of several stimuli pigeons recognize as similar or different, as will be discussed in detail in chapter 6. Although such experiments have so far been limited to restricted laboratory situations, they might be modified and extended to inquire of blackbirds whether certain aspects of a male's displays were judged to be similar to representations of abundant insects. If such experiments should yield positive results, cognitive ethologists would have obtained suggestive but significant evidence that the displays in question did convey a message relating to insect abundance.

After the young blackbirds have hatched, the mother, and in the case of the yellowheads sometimes the father as well, have an extremely demanding task of finding, catching, and carrying back to the nest a sufficient number of insects to feed their hungry young. The actual selection and capture of insect prey is difficult to study in detail, because many of the insects are small and the birds cannot always be approached closely enough while they are feeding to see just what they are doing even with the aid of binoculars. Orians and his colleagues used several ingenious

methods to determine what quantities of different insects were taken. One method was to place around the neck of a nestling a loose collar formed from a soft pipecleaner, not tight enough to prevent breathing but sufficient to prevent swallowing of insects. The accumulation of insects in the nestling's mouth was then removed for analysis after it had been fed. This procedure showed that as many as ten insects might be delivered to a nestling on one return visit by its mother.

Orians and his colleagues also learned by tedious observation and long practice to identify through binoculars many species of insects as they were captured by the blackbirds. Sometimes a bird carrying a large load dropped what it had while pursuing and usually catching an additional insect, but in such cases it always picked up the previously gathered prey and then carried the whole lot back to its young. The foraging behavior of these blackbirds conformed at least approximately to expectations based on optimal foraging theories. These predict, for example, that when gathering food close to the nest, birds should return more often with smaller loads than when they are obliged to search for food at greater distances. In the former case the return trips require less time and energy.

The adult blackbirds must also feed themselves, and they usually swallow the first few insects captured on any one foraging trip before beginning to gather food for the young. The utilization of specific types of insect prey differs to some extent according to the circumstances. When they are not feeding young, these blackbirds often eat dragonflies. The available dragonflies were quite large and provide excellent nutrition for the young; and even when they were the first insect caught on a particular sortie the parent bird did not swallow them but carried them back to the nest. What, if anything, do these busy parents think as they devote most of their waking hours to gathering food for their hungry young? Perhaps "Those youngsters need food," or "That dragonfly will stop its squawking for a while." We cannot say, as yet; but these are plausible inferences that should be kept in mind as hypotheses awaiting an adequate test.

### Oystercatchers' Mussel-opening Techniques

The oystercatcher (*Haematopus ostralegus*) is a large shore bird with a conspicuous red bill; it is related to the sandpipers and plovers. Mussels exposed at low tide are one of their principal foods, but they also feed on other shellfish and on earthworms exposed in plowed fields. The English behavioral ecologist Norton-Griffiths (1967, 1969) discovered

that on the coast of Cumbria they use two principal techniques for opening mussel shells. When the mussels are fully exposed the birds seize them with their sturdy bills, pull them loose from the substrate, and carry them to a patch of sand where they turn the shell so that its flat ventral surface is uppermost. Even though this is not the most stable position, the oystercatcher maneuvers the mussel so that it remains ventral surface up while hammering open the shell. To determine what forces were necessary for this operation, Norton-Griffiths built a mussel-cracking machine, using a close copy of an oystercatcher bill as the pick. The flat ventral surface of the shell proved to be the most easily broken part. Each oystercatcher learned where the sand was suitably hard for this operation and brought numerous mussels to the same spot.

When mussels were covered by shallow water the oystercatchers open them in an entirely different way. They search for slightly open shells and stab their bill into the opening. They do this in such a manner that they cut the large adductor muscle that closes the shell. After thus rendering the fleshy body of the mussel accessible, the oystercatcher tears the shell loose from the substrate and carries it to some convenient spot where it picks out the body of the mussel and eats it. At first this difference in feeding behavior appeared to be an adaptive adjustment to circumstances and opportunity; if the mussel shell is tightly closed, as it is when fully exposed, it must be hammered open; but when the shell is slightly opened underwater, the stabbing technique is easier. When Norton-Griffiths marked individual oystercatchers and observed their feeding behavior, it turned out that each one specialized in one or the other procedure. Further study strongly indicated that the young oystercatchers learned which technique to use when they began feeding with their parents. It seems clear that each bird learned only one of the two techniques, rather than simply playing out a genetically prescribed pattern of behavior. In many other circumstances, however, birds and other active animals must employ a variety of food gathering and processing actions according to the circumstances.

### Darwin's Finches

The finches that inhabit the Galapagos Islands provide a classic case of evolutionary diversification. Sometime within the past million years or so an ancestral population established itself on these dry volcanic islands, and its descendants evolved into thirteen species that range in size from less than 10 to more than 40 grams. They were collected by Charles Darwin and their nearly continuous variation left him some-

what confused, so that it is not clear just how influential they were in his recognition of evolution by natural selection. The history, ecology, and evolutionary biology of these birds has been recently reviewed authoritatively by Grant (1986). There are three groups of Galapagos finches, which can conveniently be categorized as ground finches of the genus *Geospiza*, tree finches of three genera, and the warbler finch *Certhiidae olivacea*. The species differ most conspicuously in the size and shape of the beak, and these differences are clearly correlated with feeding habits. Finches with short thick beaks feed on seeds, many of which are too hard and tough to be cracked by the more slender beaks of other species that specialize on insects.

Darwin's finches live in a harsh environment where food is often very difficult to obtain, except after the occasional rains when vegetation and insects become much more abundant than during the usual dry periods. Their diet tends to be opportunistic; as Grant (1986, 393) summarizes it:

As a group, Darwin's Finches rip open rotting cactus pads, strip the bark off dead branches, kick over stones, probe flowers, rolled leaves, and cavities in trees, and search for arthropods on the exposed rocks of the shoreline at low tide. They consume nectar, pollen, leaves, buds, a host of arthropods, and seeds and fruits of various sizes. . . . By virtue of their deep beaks, and the masses and dispositions of the muscles that operate them, ground finches crush seeds at the base of the bill. In contrast, tree finches apply force at the tips of their bills to the woody tissues of twigs, branches, and bark, and thereby excavate hidden arthropod prey. . . . The warbler finch, cactus finches, . . . woodpecker finch, and mangrove finch have relatively long bills which they use to probe flowers for nectar or holes in woody tissues for arthropods.

In addition to these general tendencies to specialize on foods for which their beaks are adapted, some of the Galapagos finches have highly specialized feeding habits. Woodpecker finches (*Cactospiza pallida*) and mangrove finches (*C. heliobates*) hold twigs, cactus spines or the petioles of leaves in the beak and use them as tools to pry arthropods of various kinds out of crevices. On two small islands, Wolf (or Wenman) and Darwin (or Culpepper), about 100 km from other islands of the archipelago, the sharp-beaked ground finches (*Geospiza difficilis*) have developed the most unusual habit of feeding on the blood of boobies (genus *Sula*). This habit probably began as a mutually advantageous feeding on ectoparasites; a related species of ground finch commonly eats ticks from the skin of marine iguanas some of which have ritualized displays to solicit tick removal by the birds. In other parts of the world

several species of small birds have developed the habit of feeding on parasites that they pick off the skin of large mammals.

These “vampire finches” direct their vigorous pecking selectively at the base of boobies’ feathers, most often near the elbow of the folded wing, drawing enough blood to drink. The boobies try to dislodge the birds, but the latter usually succeed in obtaining a blood meal by repeated attempts. This habit is well established on Wolf Island, but on other islands where the same species has been thoroughly studied numerous boobies also nest without any sign of its occurrence. On Wolf Island *G. difficilis* also “push and kick seabird eggs against rocks, widen cracks that form in the shell, and then consume the contents” (Grant 1986, 393).

While Galapagos finches are not the only birds with diversified and ingenious feeding habits, they demonstrate rather clearly how much versatility is required to make a living under difficult conditions. The use of twigs as probing tools, and the selective pecking at the bases of booby feathers to obtain a drink of blood are especially suggestive. It is important to recognize that the same individual finches employ a wide variety of food-gathering techniques according to the circumstances, although no one species exhibits the full range of feeding specializations displayed by the Darwin’s finches as a group. We can only speculate about the origin of feeding on booby blood, but when a finch pursuing ectoparasites that crawled deeper into the thick feathers perhaps accidentally pecked hard enough to break the skin, was it pleasantly surprised to find a source of nutritious fluid? Did this perhaps remind it of the fluids to be found and eaten from inside cracked seabird eggs?

To an inclusive behaviorist these are idle and foolish speculations, but they call to mind the extensive experiments of Tolman (1932, 1937) with laboratory rats that seemed to be surprised when food they had every reason to expect to find at the end of a well-learned maze was not forthcoming. Here we would be dealing with pleasant surprises rather than disappointments, but if and when methods are developed to test the hypothetical inference of such simple but probably vivid mental experiences, we will have learned something important about the animals concerned.

### Searching Images

When a hungry animal is searching for food under natural conditions it would waste a great deal of time and effort to scrutinize every detail of its surroundings. Both evolutionary selection and learning must exert a



strong influence on searching behavior. Animals concentrate their attention not only on things that look, sound, smell, or feel like food but also on quite different things that are signs showing where food may be available. Specialized sensory systems are sometimes employed in searching for food. For example, some sharks detect the weak electric currents from the contractions of the heart or other muscles of prey animals that would otherwise be very difficult to locate (Kalmelijn 1974). And insectivorous bats distinguish the sonar echoes of edible insects from the many other echoes returning to their ears (Schnitzler et al. 1983; Ostwald et al. 1988). But most searching is based on vision, olfaction, or hearing.

The basic idea of a searching image, or its equivalent, was discussed by many early ethologists, and in recent years detailed studies of foraging birds have shown that they look for particular patterns that reveal where food is to be found, such as the barely perceptible outline of a cryptically colored moth resting on the bark of a tree trunk (Pietrewicz and Kamil 1981). In a wide variety of laboratory experiments, rats or pigeons learn that visual patterns which ordinarily have nothing to do with food are now signals that food can be obtained. Somewhere in the animal's brain there must be a mechanism for recognizing what are termed searching images.

One of the most thorough and significant studies of searching images was carried out by Harvey Croze (1970). On a sandy beach where carrion crows were gathering mussels at low tide he laid out a row of empty half mussel shells, convex side up, and beside each shell he placed a small piece of beef. After five hours the crows had taken all the pieces. The next day Croze laid out twenty-five mussel shells and under each one he hid a similar piece of beef. When the crows returned they turned over twenty-three of the shells and ate the meat. They had learned quickly that mussel shells lying on the sand, which would ordinarily be empty, had suddenly become sources of tasty food. On the third day the meat was buried in the sand underneath the shells. The crows turned these shells over, but finding nothing directly under them dug with their bills in the sand until they found and ate the meat. Although olfaction is not well developed in birds, one cannot rule out the possibility that crows could smell meat at close range, especially since pigeons can discriminate between different odors in laboratory experiments (Schmidt-Koenig 1979). But regardless of the sensory channel employed, these carrion crows had obviously learned quite rapidly that food might be buried in the sand under empty mussel shells.

Croze now continued to place similar mussel shells on the beach, but without any meat. For some time the crows continued to turn over

these shells, but gradually paid less and less attention to them. When they were only occasionally turning over mussel shells, Croze placed bait under some. When a crow found one that was thus baited, it began turning over many more. Under natural conditions it is common for something to be a sign of food only some of the time. Animals learn that it pays to inspect such objects even though they yield food only occasionally, and, when they do yield food, to search for similar objects. Similar behavior has also been observed in other animals, as reviewed in the symposium edited by Kamil and Sargent (1981).

The signs of food availability may be difficult to recognize, for it is obviously advantageous for potential prey to avoid easy detection. But locating food is so crucial that many animals have developed not only efficient sensory mechanisms for distinguishing signs of food from very similar objects, but an ability to learn what is a fruitful searching image. This is well illustrated by the experiments of Pietrewicz and Kamil (1981), who applied to bluejays instead of pigeons the type of operant conditioning procedures developed by psychologists. Naive bluejays were adept at learning how to pick out cryptically colored moths resting on backgrounds very similar to their own appearance.

Animals cannot ordinarily predict what objects are likely to indicate the presence of food, and an ability to learn about novel signs of food is useful to many species. An interesting example grew out of the marking of nest locations by ethologists. Ground nesting birds often lay eggs that resemble the substrate on which they are laid, and some conceal their nests very effectively under vegetation. Having laboriously located such nests, ethologists often mark their location by placing stakes a short distance to one side, in order to facilitate finding them again. In one study of nesting phalaropes and semipalmated sandpipers near Churchill, Manitoba, many nests were marked by 50 cm stakes placed 2 to 3 meters southeast of each nest (Reynolds 1985). At least one sandhill crane learned that these novel objects were signs of tasty food. Reynolds observed this bird searching diligently near nest markers, and although nest predation was not observed directly, eggs were missing from nests near which there were perforations in the ground almost certainly made by the bill of a probing crane. This use of completely novel searching images indicates how versatile birds can be in learning what to look for when foraging.

### Tit Tactics

The genus *Parus* includes the North American chickadees and titmice, those acrobatic and entertaining visitors to thousands of bird feeders,

along with several European species known in England as tits. Because these birds do well in captivity and display ingenious foraging behavior, J. R. Krebs and others have studied the nature and efficiency of their feeding tactics when they search for insect prey. The stated purpose of these investigations was to test mathematical theories about optimal foraging behavior. Although the investigators did not admit to any interest in whatever thoughts and feelings the birds might have experienced, their findings provide suggestive hints.

In one set of experiments Krebs, MacRoberts, and Cullen (1972), Krebs and Davies (1978), and Krebs (1979) studied how great tits (*Parus major*) coped with the challenging problems of foraging for concealed food. In order to standardize experimental conditions Krebs and his colleagues did not study the capture of normal insect prey hidden on natural vegetation. Instead they used mealworms (larvae of the flour beetle), which are about 3 mm in diameter and about 25 mm long. Many insectivorous animals eat them avidly in captivity. To analyze both how the tits would learn to find mealworms hidden in different ways, and how several hungry birds foraging in the same area would interact, four types of hiding places were employed: plastic cups called "hoppies"; pingpong balls cut in half, called "pingies";  $7.5 \times 4.5 \times 4.5$  cm blocks of wood termed "milkies" with 1.5 cm holes drilled 2 cm deep into their tops; and "barkies," consisting of small strips of masking tape stuck on trunks of artificial "trees" constructed from wooden dowels. Under the tape there might be a mealworm forming a small bump. The milkies were designed to simulate milk bottles, which wild tits had learned some years earlier to open by tearing off the thin metal foil used to cover their tops, as discussed below.

The first three types of container were filled with sawdust or bits of paper and the openings were covered with masking tape. Only some contained mealworms, so that the birds had to open them to find whether they were or were not sources of food. To prepare the birds for this new type of foraging they were first given uncovered mealworms, then mealworms buried in sawdust in the same containers but not covered with masking tape, and, finally, covered containers. They learned surprisingly quickly that they could sometimes find food by pecking through and tearing off the tape. Some of the barkies consisted of short pieces of thick string covered with tape, but the birds never learned to discriminate between masking tape with bumps formed by mealworms or bits of string. All these experimental arrangements were designed to simulate the task faced by birds when they search through large areas of vegetation for those few spots where something edible can be uncovered by probing or pulling off layers of bark.

Except for failing to distinguish barkies concealing mealworms or bits of string, the great tits learned to forage in these new types of insect hiding place; if mealworms were provided in one type of container but not the others, they concentrated their foraging on the type that had yielded food. Individual great tits specialized in particular methods of extracting the mealworms. Some concentrated on the hoppers, turning over the pieces of paper much as wild birds turn over leaves lying on the ground, and peering into the container. Others wallowed in the container and threw out the pieces of paper. One discovered that by pecking through the masking tape he could peer into the container and see whether a mealworm was present. Some opened the milkies by hammering through the tape, while others pulled away one edge of the tape.

These individually varying patterns showed that foraging is not a fixed, stereotyped pattern, and suggest that each bird was trying various actions in its efforts to find concealed food. When one bird was allowed to discover that a particular container contained a mealworm, others housed in the same cage also began to look in similar places or similar containers. In short, these great tits learned a great deal about where to find concealed food in this novel situation both by remembering where and in what sort of hiding place they had found mealworms, and by observing where other birds found them. Once a food source had been identified, the dominant bird of a group would chase others away from it and take more food in a given time than the subordinates.

The versatility of insectivorous birds in finding hidden food items led to a spectacular development in the 1930s, when two species of tits discovered that milk bottles delivered to British doorsteps could be opened by pulling the metal foil off the tops of the bottle (Fisher and Hinde 1949; Hinde and Fisher 1951). At that time the milk was not homogenized, and the tits could drink the thick cream from the top of the bottle. Careful studies were made of the gradual spread of this behavior throughout much of England until a change in the technology of covering milk bottles eventually deprived the birds of this source of food. While the matter was not studied directly, it seemed at the time very likely that increasing numbers of tits took up this habit by observational learning—seeing that another bird had found food in a novel sort of place, just as the experiments of Krebs and his colleagues showed they could do under controlled conditions. Many behaviorists are suspicious of such suggestive evidence for observational learning, however, as recently reviewed by Galef (1988) who considers it “an onerous concept” and prefers terms such as social facilitation used by many of the early ethologists and advocated recently by Clayton (1978). Social facilitation is the stimulation by other animals that causes a given animal to

perform a pattern of behavior that it had already performed on other occasions. It differs from observational learning in that no new or modified behavior is learned by observing another animal, and it seems to avoid the implication of conscious copying, although either effect might be facilitated by conscious realization of its appropriateness. It is difficult, however, to dismiss some evidence for learning by observation, such as examples discussed in chapter 11 involving cetaceans and primates, and especially the observations of Boesch (1991) of active teaching by chimpanzees. Palmeta and Lefebvre (1985) and Lefebvre and Palmeta (1988) have demonstrated that pigeons can learn a novel food-gathering technique by watching other pigeons obtain food in this way.

The basic motions used by tits to open milk bottles were much the same as those used to pull layers of bark from vegetation. Recognition of this similarity has led many to disparage the discovery that milk bottles were a source of food as not so novel after all. Indeed it was not the development of a whole new motor pattern, but it was a case of versatile application of a previously well-developed type of action to a new and wholly different situation. This is typical of the interplay of ideas about animal behavior that has characterized advances in ethology. Some see novel behavior as evidence of radical inventiveness, a sudden insight that some completely new type of behavior will yield a desired result. Others note that the same limbs are moved in ways that are not very different from other long established patterns of behavior, and pooh-poo the animal's performance as nothing new. Sherry and Galef (1984, 1990) have studied the acquisition of very similar milk-bottle-opening behavior in captive chickadees (*Parus atricapillus*), close relatives of the British tits studied by Fisher and Hinde. They found that some chickadees learned this novel method of obtaining food on their own, but that they are more likely to do so if they could see another chickadee in an adjacent cage. But they were about equally likely to acquire the new behavior whether or not the other bird opened a milk bottle. This supports Galef's general view that learning by imitation is rare or nonexistent in animals, and that social facilitation is a more parsimonious explanation of cases like the milk bottle opening by British tits in the 1930s.

There are elements of accuracy to both views. The tits certainly did not comprehend the nature of milk bottles, the properties of glass and metal foil, or the nature and source of cream. But in hungrily exploring the environment of village streets, sidewalks, and doorsteps, they found that pulling off a sheet of shiny, pliable stuff allowed them to get at a new and tasty sort of liquid food; and they went on to exploit this new

food source. Other tits presumably picked up the habit by watching their companions, as in the experiments of Krebs and his colleagues. This is probably typical of innovation by animals; they learn that applying familiar motor patterns to new objects or in novel situations achieves a desired result or avoids an unpleasant one.

To what extent does the novelty in applying well-established actions to new situations indicate conscious thinking? The degree of novelty is surely an important factor, for the essence of the distinction between social facilitation and true observational learning is that in the former case the presence, or sometimes the food getting, of one or more other animals elicits a form of behavior already familiar to the animal in question. Although inclusive behaviorists are so averse to considering conscious thinking that they seldom phrase the distinction in such terms, what they seem really to mean by true imitation, which Galef finds "an onerous concept," is the conscious copying of another animal's behavior. How might one hope to detect conscious imitation? Possibly this might be accomplished by some form of communication in which the imitating animal conveyed to others (and thus potentially to eavesdropping cognitive ethologists) the basic thought of getting food by some novel form of behavior. Nothing of the kind has been observed to date, but it would be worthwhile to keep an open mind about such possibilities.

### Dropping Shellfish on Hard Surfaces

An enterprising sort of behavior carried out quite often by herring gulls is to carry clams, whelks, or other shellfish to some hard surface on which they are dropped from a height of several meters. Similar behavior has been observed in other birds, including crows; but it has been thoroughly studied in herring gulls. This process is quite different from finding food, seizing it, breaking it up, and swallowing. A potential food item must first be recognized as something that becomes edible only when its outer shell is broken. Then the bird must pick it up, fly with it to a suitable place, and drop it from a sufficient height. In some areas ethologists have reported that gulls are not selective and drop shellfish on soft surfaces where they do not break. But it is a common observation that herring gulls drop the great majority of the shells they carry on rocks, roads, parking lots or other places where the shells do break. The accumulation of broken shell fragments can often be found concentrated along particular stretches of a paved road. In tidal estu-

aries consisting of sand flats and salt marsh with very few rocks, those few are sometimes surrounded by a halo of clamshell fragments.

Beck (1980, 1982) studied shell dropping by herring gulls on the shores of Cape Cod, Massachusetts. These birds picked up clams, whelks, or empty mollusk shells inhabited by hermit crabs which they found at low tide, and carried them for distances on the order of 30 to 200 meters to rocky areas, sea walls, and paved roads or parking areas. Beck observed that the gulls usually flew quite low over the beaches so that during all but the last part of each flight they could not see the hard surfaces toward which they were flying. They had evidently learned where to take shellfish for this purpose. In one area 90 percent of the drops were directed at a particular sea wall which occupied only about 1 percent of the area over which the gulls flew.

Beck also observed that when dropping shells on this relatively small sea wall the gulls dropped them from lower altitudes than when using a large parking lot. Perhaps they realized that there was no danger of missing this larger target and that the shells were more likely to break from a greater height. Shells did not always break, and the gulls often picked up an unbroken shell and tried again. Beck also observed that young herring gulls were less successful than adults; they dropped rather few shellfish, but often carried up and dropped other objects, apparently in play. We have no detailed data, however, concerning the development of shell-dropping behavior.

Other studies by Zach (1978) showed that a particular population of crows nesting on an island near the coast of British Columbia had developed the habit of gathering whelks at low tide and dropping them on particular rocky areas where they often broke so that the crows could eat the soft parts. Each pair of crows foraged at one section of beach and dropped whelks on a particular rocky area. Not all rocks were appropriate, because if they were too close to the water the whelks would bounce off and sink. If the rocks were not fairly level, edible fragments fell into deep crevices where they were also lost. From a range of sizes of whelks the crows selected the larger ones and they did not pick up dead whelks or empty shells.

Zach studied the selection process by stuffing empty whelk shells either with very light material or with something similar in density to the living mollusk. He then glued back in place the horny operculum that closes the shells and found that the crow selected shells of normal weight or density. Presumably a lightweight shell would ordinarily mean a shriveled corpse rather than a fresh and edible morsel.

Zach observed that the crows dropped whelks from heights ranging

between approximately three and eight meters. Only about one in four drops broke the shell, so that many had to be picked up and dropped over and over again. Unless they were disturbed, the crows persisted until the shell finally broke, which sometimes took as many as twenty drops. Why didn't they fly higher so that shells would be more likely to break? Zach's observation suggested that the crows had some difficulty in seeing where the whelk had fallen, and after dropping one they descended in such a way that it seemed that they were watching the trajectory of the falling shell. When an occasional whelk was dropped from a greater height it also seemed more likely to shatter into several fragments, making it more difficult for the gulls to locate and pick up all the soft parts. Perhaps it was less pleasant to eat whelks containing small bits of broken shell. This was indicated by the fact that crows sometimes dipped broken whelks into freshwater pools before eating them, apparently removing fragments of shell.

Only a small fraction of the crows collected whelks and dropped them on rocks, so that this specialized feeding behavior had presumably developed quite recently. The initial stages of crows' discovery of this type of feeding and its spreading to other birds have not been studied. But Zach did observe some individual differences. For example, one crow picked up and dropped two whelks simultaneously, although all the others carried only one at a time. Such individual variability suggests that the birds had tried different tactics and were gradually learning which ones were most effective.

## Caches

Many animals store excess food when it is abundant. Curio (1976, 22–25) describes how numerous predators store captured prey for later consumption. Often when a hungry animal finds an abundance of food it stores more than when the same food is located after it has eaten its fill. This might be due to thinking about future needs even when satisfying its immediate hunger. Under natural conditions much of this stored food is recovered and eaten later, but by no means all. Other animals take some, and the animal that stored it in the first place does not always retrieve it. But a substantial fraction is recovered, by some species at least, often after intervals of weeks or months.

Squirrels are the most familiar animals that store food, but there has been considerable uncertainty as to how they recover buried nuts. Cahalane (1942) concluded that western fox squirrels do not retrieve buried nuts by memory but by smelling them. Lewis (1980) reached



similar conclusions, and it has also been suggested that, rather than remembering where they stored nuts, squirrels notice signs of the ground having been disturbed. More recently, however, McQuade, Williams, and Eichenbaum (1986), Jacobs (1989), and Jacobs and Liman (1991) found that captive gray squirrels did remember the location of some of the food they had stored in a large cage. It remains to be determined what role memory plays under natural conditions.

Birds have provided stronger evidence of recovery of stored food by means of a detailed memory (Kallander and Smith 1990). Experimental studies of marsh tits by ethologists at Oxford University have been especially revealing. These birds are very similar to North American chickadees but at bird feeders they must compete with more species of birds that eat similar foods. As reviewed by Shettleworth (1983) and Sherry (1984), two other tits of the genus *Parus*, the great tit and the blue tit tend to eat rapidly when peanuts or other desirable seeds are available. Marsh tits, on the other hand, tend to grab single seeds, fly away, store them, and quickly return for repeated storing of individual seeds in different places. They do return to the hiding places and recover many, but not all, of these seeds.

Cowie, Krebs, and Sherry (1981) studied the caching behavior of marsh tits under natural conditions by radioactively tagging sunflower seeds and detecting their hiding places with a scintillation counter. They found that stored seeds disappeared much more rapidly than control seeds stored in very similar sites by the experimenters. This suggested, although it did not rigorously prove, that the birds were recovering seeds with reasonable efficiency.

Turning to laboratory experiments where conditions could be better controlled, Sherry, Krebs, and Cowie (1981) allowed captive marsh tits to store several hundred seeds per day in a large aviary. The birds recovered stored sunflower seeds at far higher than chance levels after being kept out of the aviary for twenty-four hours. To control for other possibilities, such as having preferred types of place to store seeds and looking for such places when searching, these experimenters took advantage of the fact that in birds visual information is processed and stored almost exclusively on the opposite side of the brain from the eye where it is received. They covered one eye of experimental marsh tits and found that this treatment did not affect their rate of recovering stored seeds. But if the blindfold was shifted from one eye to the other after seeds had been stored, the birds located seeds only at approximately a chance level. This greatly strengthened the evidence that they were remembering specific locations where seeds were stored even when dozens of such places

in a large aviary had to be remembered. In further experiments of the same general type Shettleworth and Krebs found that marsh tits remembered quite well where they had stored seeds. Furthermore, when storing additional seeds they usually avoided those hiding places where they had recently placed a seed. Evidently marsh tits specialize in storing and retrieving seeds, and they are probably much better at this task than many other species.

An even more impressive example of memory for food caches has been provided by studies of Clark's nutcracker, a relative of the crows and jays, which lives in alpine environments in western North America. Food is very scarce during long cold winters, but during the autumn these birds gather enormous numbers of pine seeds and store them in crevices or bury them in the ground. This behavior has been studied in detail by Balda (1980), Vander Wall and Balda (1981), Vander Wall (1990), and Balda and Turek (1984). When seeds are plentiful a single bird may hide as many as 33,000 during the fall. Each cache contains ordinarily two to five seeds. To obtain enough food to survive through a typical snowy winter it is estimated that the Clark's nutcracker must relocate approximately a thousand of its caches.

In order to study this remarkable type of memory under better controlled conditions, captive nutcrackers were allowed to bury pine seeds in sand spread over the floors of a large aviary cage. After being kept out of the cage for a month, a nutcracker recovered and consumed a substantial fraction of these seeds. To be sure, some seeds could be found by random searching, and when the experimenters buried numerous seeds themselves, the bird found a few. But the nutcracker found many more of the seeds it had stored itself. Had it been using odor or some other cue than its memory, it would presumably have been equally able to find both kinds of seed. The cage was provided with conspicuous logs and stones on the floor. The nutcracker buried most of its seeds in the sand near such landmarks, and its success at finding them was greater than when no such landmarks were made available. But when the stones or logs were shifted during the month that the bird was not allowed in the cage, it would usually search near a certain part of a log as if it remembered the location of each cache in relation to this large and conspicuous object. Its recovery rate was very low after the landmarks had been shifted.

Under natural conditions the environment where seeds are hidden changes drastically during the winter as leaves fall and the ground is often covered with snow. The nutcracker must remember at least approximate locations with reference to relatively large and constant land-

marks such as trees or sizable rocks. Field studies have shown that nut-crackers do search even under the snow in more or less the right general locations where they have stored seeds. Presumably they remember a large number of such locations, and they may look at them from time to time as leaves fall and snow arrives to reinforce their maplike memories. When it is important for birds and other animals to remember a large number of details, they are often able to do so. To what extent they think consciously about this task is another and more difficult question. They can be regarded as thoughtless memory machines, but, as in other cases of this sort, simple conscious thinking about the task may well be helpful.

## *Predation*

**T**he complex and often dramatic interactions of actively mobile predators and their elusive prey provide many suggestive insights into what life is like for the participants in this all-important phase of their lives. For the predator, the location and pursuit of appropriate prey calls for tactics that can be rapidly adjusted to changing and often unpredictable circumstances. Although success or failure in a particular hunt is not ordinarily crucial for the predator, its survival and reproduction depend on succeeding reasonably often. Prey animals must adjust their behavior in many ways, especially to balance the need for food against the dangers of predation. For them, each encounter is literally a matter of life or death. The challenges of catching prey and escaping capture are just the sort of situations where conscious thinking may be most helpful. When predation is studied carefully under natural conditions it often turns out that the animals adjust their behavior with an adaptive versatility that suggests simple thinking about the likely results of various behavior patterns among which they must make split-second choices.

The behavior of predators and prey has come under strong selective pressure in the course of their evolutionary history. Predation and efforts to escape are widespread among animals, and some of the most thought-provoking examples suggesting conscious thinking have been described among animals that we do not ordinarily consider especially versatile or intelligent. Out of the thousands of species of predators that capture even larger numbers of other animals under natural conditions, it has been necessary to select for this discussion a few specific cases where the behavior of both predators and prey has been described thoroughly enough to provide a reasonably clear picture of their respective tactics. Much of this section is based on an excellent monograph by Curio (1976).

## Pike and Minnows

The predator avoidance behavior of small fish, especially species that aggregate into compact schools, has often been interpreted in terms of stereotyped instinctive reactions. These interactions between predatory fish and their prey has been reviewed by Noakes (1983) and Helfman (1988). As emphasized by Magurran (1986), there is actually a great deal of individual variability in fish behavior, and this variability often involves adaptation to specific local situations. Variation is the raw material on which evolutionary selection operates, and recent sociobiological theories have accounted for alternative behavioral strategies that are effective and adaptive for different members of a given species. For example, sticklebacks from lakes where pike are present are much more timid in the presence of pike than others from waters that have no large fish predators (Huntingford 1982). In waters where herons are important predators the sticklebacks spend more of their time near the bottom (Huntingford and Giles 1987). Coho salmon also adjust their feeding behavior in accordance with the availability of food and the risk of predation (Dill 1983). Groups of goldfish tend to search for food near to where other goldfish are feeding, but not near to groups that are not gathering food (Pitcher and House 1987).

The interactions of pike and minnows involve especially significant adaptive variability, as revealed by the detailed field and laboratory investigations of T. J. Pitcher, A. E. Magurran, and their colleagues. These minnows are about 8 cm in length, and they spend much of their time feeding singly or in small groups spaced some distance apart. Pitcher (1986) advocates using the term "shoal" for groups of fishes that remain together for social reasons, and "school" for those shoals in which swimming movements are synchronized and polarized, that is, all fish head in nearly the same direction.

When a 20–30 cm pike was introduced into a 1.5 × 2 meter tank where twenty minnows had been living for some time, the minnows' first response was to stop feeding and come together into a compact school, each fish about one-half to two body lengths from its neighbors (Pitcher, Green, and Magurran 1986). Earlier investigations had demonstrated that minnows in such schools are less vulnerable to predators. But then, at intervals of three or four minutes, some individual minnows or small groups began inspection behavior. They swam away from the school and approached to within four to six body lengths of the pike, paused for about a second, and then swam back to rejoin the

school, which usually then moved farther from the pike than it had been before the inspection. When a single minnow conducted an inspection it usually moved from the edge to the center of the school on rejoining it. Earlier experiments had shown that minnows have some difficulty in recognizing pike; they approach both realistic and crude model pike, but resume feeding if the model does not resemble a real pike. During inspections, the minnows avoided the most dangerous zone immediately around the pike's mouth. This behavior strongly suggests that the inspecting minnows are aware the pike is a danger and are seeking to find out whether it is actually a predator and also how likely it is to attack.

In these experiments the pike often began to stalk the minnow schools by slowly approaching them. In addition to simply swimming away from the pike, the minnows react to a stalking or attacking pike by employing several quite different tactics. One response is for one or more members of the school to "skitter" by accelerating rapidly for one to five body lengths, often moving away from the school and then returning to take up a new position. Sometimes there is a more vigorous and synchronized "group jump" during which the school moves rapidly and vertically to a new position. It seemed unpredictable to the investigators (and presumably also to the pike) which of these tactics would be employed in a given instance, a kind of "protean behavior" discussed by Driver and Humphries (1988). Another form of antipredator behavior performed by large schools is to open up a space roughly five minnow body lengths in size around the pike as it moves into the school, then close around it as it enters the open space and thus form a minnowless "vacuole" surrounding the predator.

Still another common maneuver is for the school of minnows to swim rapidly ahead of the approaching pike, then separate into two groups that turn toward the predator's tail as it passes. This "fountain" maneuver may also occur if the school meets a diver or fishing gear. As Magurran and Pitcher (1987, 453, 460) describe the behavior, "escaping fish keep one eye on the object or predator they are avoiding while maintaining a swimming track of approximately 155 degrees to its current position. This causes the school to split into two. By then reducing the angle of their swimming track to maintain visual contact with the object, the fish automatically come together in a shoal behind it." When closely approached or actually attacked by the pike the schools sometimes exhibit a "flash expansion" in which the fish appear to explode by swimming rapidly in all directions away from the center of the school.

Finally, after a school has split up, individual minnows often seek cover between pebbles at the bottom of the tank or under vegetation. Pike counter this tactic by "vigorous attempts to flush minnows out from their hiding places by directing jets of water towards them."

Similar interactions between other predatory fish and the smaller fishes on which they feed have been observed under natural conditions. For example, Helfman (1989) has recently reported a series of experiments on the responses of a small Caribbean reef fish, the threespot damselfish, to presentations of models of a local predator, the Atlantic trumpetfish. These experiments were conducted at depths of two to ten meters near coral reefs by Scuba or snorkel divers who moved a large or small model trumpetfish toward the damselfish in either a vertical or horizontal orientation. Trumpetfish were observed to strike at prey more often when in a head-down vertical position. Large and vertically oriented models were more likely than smaller or horizontally oriented models to elicit escape behavior, including entering refuges in the coral. Helfman describes several other cases where prey animals exhibit what he calls a "threat-sensitive predator avoidance." As a conventionally cautious ethologist he refrains from any speculations as to conscious intent; but the fish he and others have studied certainly behaved as though aware of differences between threatening and nonthreatening predators and reacted appropriately.

The overall impression that can be drawn from this series of appropriate maneuvers by predatory and prey species of fish is that the former are actively trying to catch the latter, and that the potential prey are well aware of the danger. On seeing a real or model pike, minnows stop feeding and aggregate into schools; individual minnows approach and inspect the pike from what seems to be a relatively safe distance; and when approached or attacked the minnows adopt a variety of evasive maneuvers that are often effective. Damselfish also approach model trumpetfish on some occasions, but both prey species avoid the head and mouth regions of the larger fish. One can postulate a complex network of instinctive reflexes to account for the observed behavior, complete with random noise generators at strategic points to explain unpredictable sequences. But the "ad hocery" of such schemes increases in proportion to the completeness of our understanding of the natural behavior. It thus becomes increasingly plausible, and more parsimonious, to infer that both pike and minnows think in simple conscious terms about their all important efforts to catch elusive food or to escape from a threatening predator.

## Drowning Prey

Predatory birds strike or seize their prey and in almost all cases kill it with the beak or talons. But in a few rare cases when a prey animal is too large to be subdued easily it is held under water until it drowns. Meinertzhagen (1959, 48) described such behavior by white pelicans (*Pelecanus onochrotalus*) in the zoological gardens near Cairo "where many wild duck take refuge by day, this pelican can be seen sidling up to a teal, suddenly seizing it, holding it under water until drowned and then swallowing it."

Two firsthand observations of prey drowning by hawks have been supported by published photographs. In the first case a female marsh hawk or marsh harrier flying low over a marshy area struck a common gallinule and fastened her talons in its back. As described by Fitzpatrick (1979), "instead of carrying the gallinule off, she pushed it down into the water which varies in depth from 2 to 10 inches in this particular area. After submerging the gallinule, the Marsh Hawk remained upright with the water midway up her breast . . . for approximately the next ten minutes. She occasionally flapped her wings and brought the gallinule up out of the water. Each time it was brought up while still alive, the gallinule thrashed about, whereupon the hawk would submerge it." Only after it ceased moving did the marsh hawk drag her prey about four feet to an exposed stump and eat portions of it.

In the second case a Cooper's hawk had seized a starling but had difficulty in killing it. As described by Grieg (1979), "I had watched the hawk struggle with the Starling for several minutes with no apparent success in some underbrush. The hawk was aware of my presence and was moving away from me and staying well hidden, but then to my surprise it carried the violently struggling Starling out into the open directly in front of me, no more than 40 feet away, and into a depression where several inches of rainwater had collected. Once in the water with the Starling, the hawk merely stood on top of it, and when the Starling would struggle to raise its head and a wing out of the water, the hawk would shift its feet so that it would push the Starling's head back under the surface." After the starling had ceased struggling the hawk carried it away. In this case the observer's presence may have disturbed the hawk to some extent, but not enough to prevent it from dispatching and carrying off its prey.

Green, Ashford, and Hartridge (1988) observed a sparrowhawk that dropped to the surface of the water after seizing a lapwing in flight. The



lapwing was held under water for about three minutes and then carried off, apparently dead. Knowing nothing of the previous history of these hawks, we can only speculate about how such behavior might have arisen, or how, or whether, they came to realize that holding a bird underwater would quiet or kill it. But it does provide a thought-provoking example of versatile inventiveness. An anonymous reviewer of this book has raised the interesting question whether a hawk that customarily captures both fishes and air-breathing birds or mammals might know enough to subdue the latter but not the former by holding them underwater. I know of no data bearing on this possibility, but enterprising ethologists might keep it in mind for future investigations.

### Predation on the East African Plains

The most abundant antelopes of East Africa are the Thompson's gazelles, or tommies, which are preyed upon by many carnivores, including leopards, lions, cheetahs, hyenas, and wild dogs. Walther (1969) and others have been able to observe many details of the behavior of the 10 to 15 kilogram tommies, because they live in open country where they can be watched throughout the day without serious alteration of their normal activities. During periods when they are migrating, they live in mixed herds with roughly equal numbers of males and females. But when they remain in one area, most herds consist of females and their young together with subadult males or "bachelors." The adult bucks defend individual territories roughly 100 to 200 meters in diameter; these are approximately contiguous with little unoccupied space between them. Groups of females move through these territories and are tolerated even when no courtship or mating is taking place. But bachelor males are chased away, and spend most of their time around the edges of the adult males' territories.

Despite the fact that tommies are an important portion of the diet of several predators, they do not appear to spend their lives in a constant state of terror. Their principal means of escape is simply running away, and this is almost always effective, provided the predator is seen at a sufficient distance. But even when lions are plainly visible the tommies do not flee unless the lion seems likely to attack. Walther states that tommies seem less disturbed by predators at a reasonable distance than by heavy rainstorms. The tommies are far from complacent, however. They watch for dangers at intervals, although any one may concentrate on grazing for many minutes at a time. The members of a herd look around at different times, so that there is almost always at least one

watching for approaching predators. As reviewed by Elgar (1989), potential prey animals such as tommies spend more time apparently watching for predators when they are in small groups than when many are within view of each other. Elgar stresses that many other factors influence time spent in "predator vigilance," but it seems clear that such watchful behavior helps avoid predation and that other group members benefit when one notices a sign of danger.

When a tommy sees something unusual or suspicious it becomes obviously alert; it holds its head high, the ears pointed forward, muscles tensed, and it looks toward whatever has aroused its attention. Sometimes a tommy in this situation stamps on the ground with a foreleg, and often it emits a soft snort which Walther describes as a "quiff." Quiffs seem to occur only or at least primarily when something has alerted the tommy, and they cause others to assume the alert posture and look in the same direction.

When a serious attack does occur, the tommies flee at a steady gallop which can attain speeds of 45 to 60 km per hour. This is faster than any of their predators can run except for a very short distance in an initial charge. But tommies often run in other ways, including stotting, in which they jump a meter or so into the air, holding their legs relatively stiff. Stotting usually occurs at the start of a chase, but only when the pursuer is not too close, and at the end when the predator has given up. When a herd of tommies is closely pursued, most or all of them bounce about in an irregular fashion, and this behavior seems to confuse many predators and hinder their concentration on a single gazelle so that often they all escape. But when closely pressed the tommies always gallop. The type of gait also varies according to the type of predator; stotting is much more common when tommies are chased by hyenas or wild dogs, but is employed rarely with lions, cheetahs, and leopards, which achieve higher speeds in their initial charge. Caro (1986a, 1986b) has analyzed stotting in detail and concludes that its most probable function is to warn predators that they have been detected or, in the case of fawns, to alert the mother that the fawn needs protection. FitzGibbon and Fanshawe (1988) have provided additional evidence that stotting shows the tommy to be in good physical condition and likely to outrun a pursuing predator.

Just before tommies are actually captured they often change direction rapidly, doubling back like a hare, but in all such cases closely observed by Walther the predator caught the gazelle in the end. When a mother and fawn were approached by a jackal, which is about the size of a fox, they would at first run off together. But sometimes the mother would

attempt to defend her fawn by charging at the jackal and striking it with her horns. Occasionally a second female, perhaps an older sister of the threatened fawn, would join in this kind of attack. Mothers with young fawns sometimes attack quite harmless animals and birds. But when the fawn is chased by a larger and more dangerous predator, such as a lion or cheetah, the mother moves about excitedly at a considerable distance without intervening directly.

Hans Kruuk (1972) describes a sort of distraction behavior by mother tommies directed at hyenas that were chasing their fawns. They would run between the two, crossing in front of the hyena and staying very close beside it but just out of reach. Although usually only one female, presumably the fawn's mother, would engage in this sort of behavior, sometimes as many as four would run close to the hyena at the same time. Yet all these efforts seemed to be ineffective. On twelve occasions fawns were aided by distracting efforts of adult females, but six of them were caught. In nineteen cases observed by Kruuk the females made no attempt to distract the hyena, yet only five of these fawns were taken. Possibly the females could discriminate between more and less serious dangers to a fawn and engaged in the distraction efforts only when the danger to the fawn was acute. If so, the two sets of data may not have been strictly comparable.

Such seemingly hopeless behavior as that displayed by an adult female tomy entails a real risk that the hyena will capture her as well as the fawn. In strictly evolutionary terms, these attempts to save the fawn appear to be maladaptive inasmuch as they do not seem to lower the likelihood that the fawn will be killed. Likewise the final frantic efforts of a tomy to escape have no statistical survival value if they are ineffective. This apparent lack of any survival value leads inclusive behaviorists to disparage the significance of such behavior, because their concern is limited to ways in which behavior contributes to the inclusive fitness of the animals in question. But when we broaden our horizons by considering what life may be like to the animals themselves, it is not surprising to find that they make strenuous efforts to avoid being killed, or having their offspring killed, even when such efforts have little or no chance of success. This is an example of how our theoretical concepts can be broadened by a consideration of how life may seem to the animals themselves.

Wildebeest attacked by a pack of hyenas make surprisingly few and ineffective attempts to defend themselves. Kruuk (1972, 158) states that a wildebeest beset by a group of hyenas makes some attempts to butt its attackers, but that "generally speaking, the quarry just stands

uttering loud moaning calls and is torn apart by the hyenas. It appears to be in a state of shock." Although cow-sized wildebeest sometimes try to escape by running into a lake or stream, the hyenas almost invariably manage to kill them. They may hope, although vainly, that they can escape by running into the water.

Mother wildebeest often attack hyenas that are threatening their calves, but those without calves hardly ever do so. Yet Kruuk observed one striking exception on the part of a cow that was in the process of giving birth. Her calf's front feet had already emerged, but she nevertheless went to some lengths to attack a hyena that was walking past and that seemed not to be paying any attention. Shortly afterwards this cow appeared to be avoiding the hyenas in the vicinity as she selected a quiet spot, surrounded by other wildebeest, where she lay down to complete the birth. Might such a cow realize that her soon-to-be-born calf was in danger of attack by a hyena? We cannot tell, but perhaps it is best to keep an open mind and not dismiss such possibilities out of hand.

### Mutual Monitoring by Predators and Prey

Potential prey animals are almost constantly on the watch for dangerous predators, and once one appears they keep it under close observation. Only on rather rare occasions does the predator become serious about attacking, and only then, ordinarily, do the prey animals become seriously alarmed. When predators and prey can see each other, they spend most of their time monitoring each other rather than in attacking or fleeing. This involves making subtle distinctions; predators notice slightly abnormal behavior that signals weakness or vulnerability. And prey animals notice the changes in the behavior of predators that signal likelihood of attack. It would be advantageous for predators to conceal such signals; therefore, they are probably unavoidable and inadvertent.

When Thompson's gazelles detect a predator, they often do not flee but move closer. They appear to be much interested and to be inspecting the dangerous creature. Walther sometimes saw a herd of tommies recognize a predator at 500 to 800 meters and then approach within 100 to 200 meters. Under these circumstances the herd contracted into a smaller area than when feeding, the individuals remaining closer to one another. When the predator moved, the herd followed it, evidently aware of the danger and ready to dash off at the first sign of an actual attack. The predators also seem to understand the situation and rarely attack a group of alert tommies. Predator monitoring by territorial males was especially evident. At the approach of a predator in daytime

the females generally moved away, while the buck stayed in his territory and kept the predator under close watch. As it moved he usually followed at a safe distance until it reached the territorial boundary. Then one of the neighboring territorial males would take over the monitoring of the dangerous intruder. This sort of predator monitoring was so effective that predators captured only one of fifty territorial males that Walther studied intensively during a two-year period.

George Schaller (1972) describes other examples of prey animals monitoring the behavior of predators and not appearing to be frightened unless the predator rushes at them directly. When a lion is walking along steadily, tommyes, zebras, wildebeest, and other potential prey usually face the danger in an erect posture but do not run away. Wildebeest usually keep up an incessant grunting, but when a lion approaches they stop, so that the predator is surrounded by a zone of silence, which undoubtedly warns others of the danger. A group of wildebeest may even approach a predator and line up to watch it pass. But if a lion stops and turns in their direction, the grazing animals usually flee for a short distance, then turn and stand watching again. Roughly thirty meters from a lion seems to be considered a safe distance in open country, but when potential prey animals move into thick vegetation they behave much more cautiously. These sensible adjustments of prey monitoring behavior suggest a conscious understanding of the relative dangers of various predators and how these dangers vary with circumstances, especially with the behavior of the predator itself.

Predators are thought to select for attack members of a herd that are weak, sick, very young or very old, although an extensive review of the evidence bearing on this question showed that the results of many investigations failed to support this widely held belief (Curio 1976, 113–17). Even when all members of a herd appear to be healthy and vigorous, hungry predators still manage to capture some. Much other evidence reviewed by Curio (117–28) does indicate that unusual or conspicuous members of a group of prey are more likely to be taken by predators. Kruuk observed that hyenas appeared to be quite adept at noticing slight differences in an individual prey animal's posture, locomotion, or other behavior indicating weakness or vulnerability. He reports that when a gazelle had been anesthetized for study or marking, he had to stand by in his automobile to protect it from attack by hyenas even after it seemed to have recovered completely and to be behaving normally. Thus while the tendency to select more vulnerable prey may have only a small overall statistical effect, it seems reasonably clear that

predators often try to identify and attack those prey animals that are most easily captured.

This ability to perceive very minor changes in the behavior of another animal appears to be widespread among both predators and prey. The same basic neurophysiological mechanisms that permit such subtle discriminations are probably called into play when animals such as Clever Hans learn to respond to minor and inadvertent counting movements of their human trainers, as discussed in chapter 1. Recognizing how basically important such discriminative perception is to wild animals under natural conditions helps us to understand how a horse or a dog can notice when a man stops counting as he watches the performance of an animal that is supposed to be solving arithmetical problems.

Kruuk observed that predators whose home area was close to that of territorial tommies never hunted these familiar neighbors. Some hyenas usually rested from midday until late afternoon in dens located within territories of male tommies. When they left their dens in the early evening they were presumably hungry; but, although they were often surrounded by tommies, they passed between them and hunted in other areas. Perhaps the hyenas knew that the local tommies were alert and difficult to catch. Regardless of that possibility, these hyenas were clearly distinguishing some tommies that were neighbors and were not attacked from others that were treated as prey. Thus their behavior was far from being a stereotyped set of responses to a particular species.

A special case of predator monitoring that involves an unusual sensory mechanism has been described by Westby (1988) in the course of extensive field studies of electric fishes. The electric eel (*Electrophorus electricus*) is well known for its powerful electric organs that can stun or kill other animals. It has been customary to consider these as defensive measures, but it has also been known for some time that electric eel are predators, and that their strong discharges help them to catch prey. Westby had placed recording electrodes in a stream and was monitoring the social behavior of a small species of weak electric knifefish, *Gymnotus carapo*, which uses its weak pulses both for orientation and for communication in courtship. While he was thus monitoring electric activity in the stream, the pulses of a 1.8-meter-long electric eel could be detected approaching the location of the knifefish. The latter stopped emitting its pulses most of the time, but was detected and devoured by the electric eel, which probably located it by recognizing its occasional weak electric signals.

In a laboratory tank a captive electric eel emitted its strong "preda-

tory” shocks when stimulated either by a live knifefish or by electrodes generating signals recorded from the same knifefish and played back into the water at normal intensity levels. Although such electric signals are unfamiliar to us, they are easily monitored and reproduced, so that the investigation of social communication and electric shock predation can be conducted with more precise control of the signals than is possible with most other animals. This offers a potentially exciting opportunity to cognitive ethologists to analyze not only predatory shocks and efforts to avoid them but also a whole range of social communication of weakly electric fish by electrical recording, analysis, and playback, as is already being done by several investigators including Westby (1988) and Bratton and Kramer (1989).

### Playing with Prey

Foxes, like many other predators, sometimes play with captured prey; while our human sympathies go out to the tormented victim, the predator seems to enjoy this sort of behavior. Henry (1986, 136–40) describes a highly suggestive incident in which a six-month-old red fox that he had observed extensively appeared to release a captured shrew intentionally and return it to the vicinity of its burrow. This fox had caught and immediately eaten one mouse, then caught another with which he “played vigorously for several minutes.” After killing it, the fox carried it some distance and cached it. Although this showed that the fox was no longer very hungry, he soon captured a shrew, which he carried some distance to an open roadway where he began to play with it. As Henry described the fox’s behavior in his field notes, “the fox is leaping around, dancing about the shrew who runs over to one side of the road before the fox herds it back to the center. After 45 seconds of playing with this animal, the fox then does an extraordinary thing. He picks the shrew up in his mouth, walks back down the slope to where he captured the prey, and then with a toss of the head spits the shrew out directly at a small burrow. In less than a second, the shrew disappears into the hole and is out of view.” Shrews have an unpleasant odor, and though they are eaten by hungry foxes, they are more often cached. As Henry suggests, this fox may have returned the shrew to the burrow a few inches from where it was captured with the anticipation that it might provide food or fun on some future occasion. Of course, we cannot be at all sure of such a suggestion, but, as Henry concludes, “if we are going to understand red foxes completely, in all their depth and breadth, we cannot study and analyze just their common behaviors.”

## Cooperative Hunting

Many carnivorous mammals sometimes hunt in groups, although it is not clear how much this increases their total food intake over what each could capture individually. Sometimes group hunting succeeds in surrounding or concentrating prey that would otherwise be more likely to escape. This type of simple cooperation has been observed when pelicans, cormorants, South American otters, dolphins, or killer whales are pursuing fish (Curio 1976, 199–201). The behavior of large cooperating groups is quite different from that of individuals pursuing fish on their own or in smaller groups. For example, Bartholomew (1942) observed that double-crested cormorants (*Phalacrocorax auritus*) fished in a different type of formation when in very large groups of 500 or more than when only 50 or so were pursuing fish together. In such cases the individuals modify their behavior only enough to maintain an appropriate position in the formation.

Meinertzhagen (1959, 47) vividly describes this type of cooperative hunting by Dalmatian pelicans (*Pelecanus crispus*) as follows: "There were over a hundred birds forming line, diving towards shore in shallow water, two ends of the line advancing in perfect order and not very fast. A crescent was eventually formed, every bird keeping his correct station, and then, as water barely 18 in. deep was reached, the two horns of the crescent increased speed, closed in, and formed a complete circle, the birds almost touching. Within the circle the water boiled with small fish, heads were rapidly plunged in simultaneously and pouches filled with fish, the circle closing in all the time and feet paddling hard to prevent fish escaping below body-line." Würsig (1983) has described how dusky dolphins herd anchovies in the open ocean, diving and swimming at them from below and from the sides while vocalizing loudly. This results in a tight ball of anchovies; and the dolphins take turns swimming into the aggregation and seizing fish while others continue the herding from outside the ball.

Chimpanzees ordinarily feed on fruit, leaves, flower blossoms, seeds, and insects. But on occasion they actively hunt, kill, and eat monkeys, bushpigs, small antelope, rodents, and even human babies. In some cases they prepare to hunt monkeys by watching them for some time, and apparently communicating with each other by low intensity sounds and touching each other. Then they approach and pursue particularly vulnerable individual monkeys, such as females or young, with many signs of intentional cooperation, as described in detail by Goodall (1986) and by Boesch and Boesch-Ackermann (1991).



In many cases the advantage of group hunting seems to be that it permits the killing of a large prey animal that would be able to defend itself against a single attacker. Hawks and eagles that prey on birds have been suspected of cooperative hunting, but when such hunting has been studied carefully it has often been unclear whether it was advantageous, or whether the same birds obtained just as much food when hunting singly. In the case of Aplomado falcons (*Falco femoralis*) in Mexico, however, Hector (1986) found that there was some division of labor and simple coordinative signaling. Bednarz (1988) has both reviewed earlier studies suggesting cooperation and reported his observations of Harris' hawks in New Mexico, which engaged in effective teamwork when hunting cottontail rabbits and jackrabbits.

These hawks, which average about 850 grams in weight, hunted during the nonbreeding season in groups of two to six, probably members of a genetically related family. They captured both cottontail rabbits, somewhat smaller than themselves, and also jackrabbits that weighed about 2100 grams. Bednarz had previously attached radio transmitters to at least one hawk in each hunting group, and he could observe the others visually during most of thirty successful hunts in which a group of hawks captured seventeen cottontails and nine jackrabbits. Cooperative hunting seems to be advantageous for Harris' hawks, since single hawks were not seen to attack large prey during these observations. Especially with jackrabbits that are more than twice the size of the hawk, it seems unlikely that a single bird would have much success. The full sequence of hunting behavior was observed in thirteen cases.

At the beginning of a hunt a group of five or six hawks would split up into smaller groups of one to three that appeared to search for prey during 100 to 300 meter flights from one conspicuous perch to another.

In seven of the thirteen well-observed hunts several converged from different directions on a rabbit that was away from cover. In four captures of a cottontail rabbit "a flush-and-ambush strategy was employed. Here, the hawks surrounded and alertly watched the location where the quarry disappeared while one or possibly two hawks attempted to penetrate the cover. When the rabbit flushed, one or more of the perched birds pounced and made the kill." The two remaining hunts that could be closely observed were relay attacks, which Bednarz describes as follows: "This technique involved a nearly constant chase of a rabbit for several minutes while the 'lead' was alternated among party members. A switch occurred when the lead hawk stooped at the prey and missed, at which point the chase was continued by another member of the party. I

recorded one relay chase that continued for at least 800 m and involved more than 20 stoops and hence switches in the lead.”

Another clear advantage of cooperative hunting is the ability to take very large prey that a single predator could not subdue unaided. One intriguing example is the hunting behavior of the South American giant otter *Pteronura brasiliensis* studied in the Manu National Park of Peru by Munn (1988). These otters are six feet long and weigh about 30 kilograms. Their principal diet consists of fish caught singly by individual otters, but they often hunt in groups when pursuing large prey. A common cooperative fishing tactic is to swim together in a loose phalanx, and dive together for ten to twenty seconds, with much thrashing and churning of the water. Sometimes groups of giant otters kill and eat black caimans from 0.6 to 1.5 meters in length, and even anacondas up to 2.7 meters long. They attack caimans almost simultaneously from several directions, and when attacking a large anaconda two or more otters would bite the snake at different points along its body, holding fast and bashing it against fallen tree trunks in the water. These group attacks are coordinated to at least a limited degree, and some quick and sensible thinking about where and how to bite in relation to where one's companions are attacking a large antagonist would seem helpful.

Kruuk (1972) summarized the results of his extensive observations of hyenas hunting wildebeest calves both individually and in groups. Only about one third of 108 attempts by one or more hyenas to capture calves were successful. Single hyenas were almost always driven off by the mother, but when two hyenas were involved one often seized the calf while the mother was attacking the other. It is also clear from many observations that hyenas and wild dogs are more successful in hunting tommyies in groups than singly. George Schaller's extensive studies of lions showed several cases in which a group of four or five lionesses spread out as they approached one or more gazelles, those in the center of the group approaching more slowly than those at the edges, thus creating a U-shaped formation that tended to surround the prey on three sides. Some prey animals escaping from lions in the center of the formation seemed to be more easily caught by those advancing on the edges of the formation. Yet both Schaller and Kruuk and more recently Scheel and Packer (1991) are very cautious about inferring conscious intent on the part of the cooperating predators. For example Schaller's index does not include the word "cooperation."

Schaller concluded that each lioness behaves more or less independently although of course quite ready to take advantage of another's

hunting efforts, as when a gazelle fleeing from a companion runs close to the lioness in question. But Schaller did note that when hunting in groups the lionesses look at each other and seem to be trying to maintain an effective formation, such as the U-shaped pattern. Groups of lionesses that hunt together routinely for months at a time are often sisters or mother and daughters, and they certainly know each other intimately. Yet like so many other ethologists, Schaller and Kruuk seem to be leaning over backwards to avoid any suggestion that lionesses or other predators intentionally cooperate by coordinating their hunting tactics.

I once had the good fortune to observe a group lion hunt involving more definite evidence of coordination. While I was briefly visiting Robert Seyfarth and Dorothy Cheney Seyfarth during their studies of vervet monkeys in the Amboseli National Park in Kenya, they drove me along a dirt road at the edge of a forested area bordering a large open plain. At a place where the woodland receded for a few hundred meters, the road ran between a semicircular area of grassland on one side and the open plain on the other. A large herd of wildebeest had split into two groups; fifty to sixty were grazing on the woodland side of the road, while the remaining hundred or so were feeding on the open plain about 150 to 200 meters from the road.

As we paused to watch the wildebeest, four or five lionesses approached with a businesslike gait along the edge of the plain, roughly parallel to the road and within a few meters of it. Both groups of wildebeest obviously saw them, for they stopped feeding and watched the lionesses intently. Because the ground was irregular we could not see the lionesses all the time, but when about 200 meters from the two groups of wildebeest two climbed slowly to the tops of two adjacent mounds where they sat upright, and remained stationary but conspicuous. After a few minutes had passed we could make out a third lioness slinking, her belly pressed close to the ground, along a ditch that paralleled the road. Although she was visible to us only occasionally, it was clear that she was moving toward a position roughly midway between the two groups of wildebeest. She soon crawled out of our view and for several minutes nothing seemed to be happening at all.

Suddenly a fourth lioness rushed out of the forest behind the wildebeest on the woodland side of the road. Although we had not seen her do so, it seemed almost certain that she was a member of the same group, and that she moved into the wooded area out of our view, and presumably also that of the wildebeest. In any event a lioness rushed

from the woods directly toward the wildebeest that were located between the woods and the road, and they thundered off directly away from her toward their companions on the open plain. This route took them across the ditch close to where we had last seen the lioness slinking furtively a few minutes earlier. As the herd bounded over the ditch she leaped up and seized one of the fifty or so that were galloping all around her. As the dust settled she was busy killing this wildebeest by covering its mouth with hers as it lay on its back, legs kicking gently in the still dusty air.

The two lionesses that had been sitting quietly on their mounds and the one that had chased the wildebeest towards the ditch walked slowly towards the downed prey, but arrived only after its kicking had ceased. All four then began to eat their prey in a leisurely fashion, and after a few moments a jackal joined the scene. Meanwhile the whole group of wildebeest returned from the open plain where they had all fled and stood in a line watching the lionesses and her victim from a distance of about a hundred meters.

A single observation such as this one cannot be taken as conclusive proof of intentional cooperation, but it is certainly very suggestive. Why else should the first two lionesses have climbed to conspicuous positions and waited where the wildebeest could easily see that they presented no serious danger? Why should a third lioness sneak so furtively along the ditch to a position about midway between the two groups of wildebeest? And was it a pure coincidence that a fourth lioness disappeared from the group and that a lioness just happened at the appropriate time to rush out from a suitable point at the edge of the forest so as to chase the wildebeest over the ditch where one of her companions was waiting? The individual elements of group hunting behavior I have described have been observed by others, but we were remarkably fortunate to see so much of this sequence. Yet the ethologists who report detailed observations of lion behavior have been so reluctant to infer conscious intent to cooperate that they seem to have refrained from reporting as much of this type of behavior as they have actually observed.

Stander (1992) has observed dozens of group lion hunts in very open country of Namibia. He studied these lions so intensively that he could recognize individuals, some by natural markings, and some by tags and radio transmitters that were attached to them when they had been captured and anesthetized. In numerous group hunts of large prey particular lionesses took the same position within a roughly linear hunt-

ing formation night after night. Individual lionesses occupied the same position (center or one of the wings) on successive nights. These formations approached prey in a coordinated fashion before the group attacked at about the same time from different directions. But hunting tactics were varied according to the situation, with smaller prey hunted by individuals in many cases.

## *Construction of Artifacts*

A wide variety of animals display considerable ingenuity in the construction of shelters and structures that serve other purposes, such as capturing prey or attracting mates. These activities require adjustment of behavior to the local situation, to the materials available, and to the various stages of construction. This necessary versatility often suggests that the animal is thinking about the results of its efforts and anticipating what it can accomplish. For acting to attain an intended objective is a more efficient process than blindly following a rigid program. This chapter discusses selected cases where animals build more or less fixed structures that benefit them or their offspring; chapter 5 describes the construction and use of tools. Although there is no sharp distinction between artifacts and tools, the details of the behavior involved in their construction and use make it convenient to discuss them separately.

The many types of structures built by animals are often characteristic of the species to which they belong, and in some cases such as the termites and the larvae of caddis flies the structures may be more useful for identifying species than is the morphology of the animals that build them. This species specificity suggests genetic programming of a relatively stereotyped nature; but when analyzed carefully the animals often display considerable versatility in adapting the details of the artifact construction to the particular situation. Karl von Frisch (1974) reviewed many significant examples in a delightful book, *Animal Architecture*. It is no accident that the same brilliant scientist who discovered that honeybees communicate symbolically, as discussed in chapter 9, also turned his attention to the ingenious variety of shelters constructed by various animals. For it is difficult to repress one's admiration for the effectiveness, and beauty, of many of the structures built by even rather simple animals. Our admiration may stem in part from the suspicion that the animals may do their building with at least some rudiments of

intention. A very thorough survey of animal architecture has been provided by Hansell (1984); this adds much detail and many new discoveries to von Frisch's more general book. The examples discussed below are based largely on these two books.

Even some of the protozoa build simple cases, usually by secreting material from the cell surface. A few, such as the amoebas of the genus *Diffugia* add external grains of sand to their outer surfaces, so that they come to resemble tiny croquettes. These particles are transported through the cytoplasm and distributed fairly evenly at the cell surface. But the processes involved appear to have more in common with cellular functions such as pinocytosis, where the cell membrane bulges out and engulfs an external particle than with active manipulation by the organism of objects outside of its body (Netzel 1977). Since protozoa lack anything at all comparable to a central nervous system capable of storing and manipulating information, it seems highly unlikely that they could be capable of anything remotely comparable to conscious thinking.

Hansell (1984) reviews several scattered examples of multicellular annelids and molluscs that build simple structures, such as the burrows of marine polychaete worms. Impressive structures are built primarily by arthropods and vertebrates. Several species of crabs dig burrows, and some fiddler crabs of the genus *Uca* add hoods near the burrow entrance, apparently as a part of their courtship and attraction of females (Crane 1975; Christy 1982). Several species of fish build nests to shelter their eggs, the most thoroughly studied being the European stickleback, whose courtship behavior has been analyzed by Tinbergen and many others. A less well-known case is the weakly electric fish *Gymnarchus niloticus*, the species used by Lissmann in his classic experiments demonstrating the use of weak electric fields for orientation. These relatively large freshwater fish build a nest from floating vegetation which has a corridor leading to a chamber at the end where the eggs are laid (Bullock and Heiligenberg 1986).

## Ant Lions

Simple pitfall traps are constructed by two distantly related groups of insect larvae, the ant lions and worm lions. Both dig shallow, roughly funnel-shaped holes in loose soil and wait with their bodies almost entirely buried at the bottom of the cavity for other small animals to fall in. The commonest prey are ants, which generally attempt to escape from the pit by climbing up the steeply sloping walls (Wheeler 1930;

Topoff 1977; Heinrich 1984, 141–51). When an ant or other small prey animal falls into the pit, the predatory ant lion or ant worm seizes it with its mandibles and injects a poison which kills the victim. Often active prey such as ants crawl about actively enough that they are not seized on the ant lion's first attempt. The ant lion then throws grains of sand in the general direction of the prey, and this seems to increase its chances of capturing an ant. Recently Lucas (1982, 1989) has studied in detail one species of ant lion *Myrmeleon crudelis* in Florida. The pits are not perfectly conical but have walls that slope more gradually in the parts of the pit where the ant lion waits for prey. The walls are steeper in front of it, and these front walls also tend to be lined with finer grains of sand.

These predatory insect larvae thus construct a very simple artifact, the pit with somewhat different walls on different sides and also throw sand grains as a very crude form of tool. The details of their prey-catching behavior are difficult to study because everything happens too fast for the human eye to follow easily. It is not clear how adaptable the ant lions are, but they do alter their behavior to some degree according to the type of prey the kind of soil in which their pit is dug, and occasionally they show interesting interactions. Wheeler reviewed earlier observations in which two ant lions dug pits so close together that an insect escaped from one pit only to fall into the other. In this case the first ant lion emerged from its pit and pursued the prey into its neighbor's pit.

### Caddis Fly Cases

One of the more impressive examples of complex structures built by very simple animals are the cases and nets built by the larvae of caddis flies. These are abundant animals in freshwater streams and ponds and many of them construct shelters of various types attached to vegetation or the bottom of whatever body of water they occupy. They develop from eggs laid in the water by winged female caddis flies which emerge and mate after a long period as aquatic larvae. The larvae of North American caddis flies and the cases they construct have been described in detail by Wiggins (1977), who illustrates numerous variations in caddis fly case and net construction characteristic of the numerous genera and species. The larvae themselves are rather nondescript and difficult to identify, but the shelters are so characteristic that they are often used by systematic entomologists for species identification. The cases built by caddis fly larvae may employ bits of leaves, particles of sand, or other



available materials including the empty shells of very small snails. They are cemented together by silk secreted from glands on the larva's head. Sometimes caddis fly larvae crawl out of their cases, and they may fight over cases or one may evict the occupant of a case and take it over (Otto 1987a, 1987b; Englund and Otto 1991).

Like other insects, these larvae grow through successive stages in which the exoskeleton is shed. In early stages the small larva uses minute and ordinarily homogeneous particles to form a roughly cylindrical case around its body. These cases may increase the flow of water over the gills (Williams, Tavares, and Bryant 1987), and also protect the otherwise vulnerable soft bodied larva from small fishes or other predators such as immature dragonflies. The case is not totally impervious; it has an opening at the posterior end to allow feces to pass out, and water circulates freely from an anterior opening to the posterior one so that the gills can extract oxygen from the water. In many species the case is portable and is carried about as the animal moves by pushing its head and thoracic segments carrying the six legs out through the front opening. The case is held close to the body by hooklike projections from the abdominal segments. In constructing their cases, caddis fly larvae are somewhat selective about the materials used. Some species cut pieces from the leaves of aquatic plants and others construct fine meshed nets that serve to strain minute animals and plants from the flowing water.

The case building behavior of a few species of caddis fly larvae has been studied carefully in the laboratory by Hansell (1984, 1968). He conducted detailed observations and experiments with *Silo pallipes* which begins its larva life by constructing a simple cylindrical tube of sand grains cemented together. This species passes through five instars between which the animal sheds its external skeleton and grows a larger one. In its first instar the *Silo* larva occupies a roughly cylindrical case composed of particles about one-half millimeter in diameter. But toward the end of this instar it adds two larger sand grains at the sides of the front end. During the second instar it adds two more larger particles, and through the three succeeding instars it selects at each molt larger grains of sand for the anterior opening. At the end of the fifth instar the case is about ten millimeters long and the larger anterior grains are two to five millimeters in diameter. Throughout this growth the larva enlarges its cylindrical case by adding more small particles.

Hansell's observation showed that the larvae reach out of their cases and feel particles in the immediate vicinity with their anterior appendages and reject many that are either too large or too small. Having felt one of appropriate size they move it into position and secrete silk to

fasten it there. On a very small size scale this behavior is flexible and adapted to the available particles and the stage of case construction.

Hansell (1972, 1974) also studied another species of caddis fly larva, *Lepidostoma hirtum*, which constructs cut panels from bits of leaves to form a floor, roof, and two sides. All of the panels are approximately rectangular pieces, one or two millimeters in size held together at the edges by secreted silk. The resulting case is strengthened by a staggered arrangement of the pieces. Each joint between two side plates intersects with the middle and not the edge of a roof plate. When Hansell cut away the front end of a case to form a continuous, smooth front edge, the larva cut leaves of different shapes from those normally used and glued them into place so as to restore the staggered arrangement. These simple insect larvae thus exhibit a considerable degree of versatility not only in the initial construction of their cases but in repairing them. Despite our customary assumption that insect larvae exhibit only stereotyped behavior, they have highly organized central nervous systems with hundreds of neurons and synapses that appear quite capable of organizing relatively complex and flexible behavior.

Yet another species of caddis fly larvae construct a more elaborate case, which provides not only a shelter but a food-gathering mechanism as described in detail by Wallace and Sherberger (1975). This case is a chamber considerably larger than the animal's body and roughly oval in shape. From the upstream end rises a tubular extension with a roughly ninety-degree bend and an opening facing into the direction from which water is flowing. From the other end of the oval chamber rises a shorter outlet tube. The entire chamber is only two or three centimeters in length, but the flow of water by the surrounding stream serves to ventilate it fairly well due to its construction. Opening into the side of the main chamber is a separate tubular structure corresponding to the normal caddis fly case. But both ends of this open into the larger chamber. The end where the larva places its head opens into the upstream side of the main chamber, and water flows through this side chamber past the larva's gills and out a posterior opening into the downstream part of the main chamber. Finally, the larva constructs a fine mesh net across the middle of the large chamber. Small animals and plants are caught on this net and serve as food. The entire structure is roughly comparable in complexity to the nests of many birds.

It has been customary to view such artifacts as caddis fly cases in much the same light that biologists view the elaborate structures of animal bodies—patterns regulated primarily by genetic instructions. But on close examination it turns out that even simple creatures such as cad-

dis fly larvae adjust their building behavior in ways that would seem to be aided by simple thinking about what they are doing. Such thinking might be limited to seeking to match some sensory or perceptual pattern that was itself produced by genetic instructions. But, as I have pointed out elsewhere (Griffin 1984), the fact that a central nervous system operates in a certain way because of genetic instructions does not necessarily mean that its operations may not also lead to cognition and perceptual consciousness.

## Insect Nests

Numerous species of insects construct a wide variety of nests or shelters as reviewed by von Frisch (1974). Often, as in the conspicuous nests of wasps and hornets, numerous females contribute by gathering bits of vegetation, chewing them, and mixing them both with saliva and with silky secretions from specialized glands or with their own feces. The resulting daubs are then applied to some solid substrate, and other daubs are added to build up a multichambered nest much larger than the individual insects. In some ways the nests built by solitary bees and wasps are even more impressive, because they result from the work of a single female. When ready to lay eggs she searches widely for suitable materials and brings them from a considerable distance to prepare a place where she builds a nest.

The mason bees of the genus *Chalicodoma* moisten with their saliva particles of sand and dirt they have gathered and form these into small oblong pellets. The female then carries each such pellet to a spot on a large rock, where she cements them together into a roughly cylindrical cell open at the top. In each cell she lays one egg and regurgitates liquid honey around it. Then she closes the top with additional sand grains, cementing it securely with saliva. Next she applies dust particles to the outside of a group of such cells with the result that they come to look almost exactly like the surface of the rock to which they are attached. The mixture of fine dust particles and saliva dries into a structure almost as hard as the rock.

A different species of mason bee, *Osmia bicolor*, seeks out an empty snail shell and deposits both her eggs and food for the larvae that will hatch from them in the narrow inner parts of the spiral chamber. Some of the food thus deposited is a semisolid mixture of pollen and regurgitated stomach content known as "bee bread." After depositing numerous eggs and a quantity of bee bread the female *Osmia* fills the middle

portion of the tapering spiral cavity of the snail shell with chewed up pieces of leaf. Nearer the outside she deposits enough small pebbles to form a fairly rigid wall. Neither the leaf fragments nor the pebbles provide a totally airtight seal, and air can still circulate even after a second wall of leaf pulp is added outside of the pebbles. As though these preparations were not enough, the mason bee adds dry stalks of grass, tiny twigs, or pine needles, piling them over the snail shell in a large irregular dome.

These elaborate sequential actions may well be genetically programmed to a considerable extent, but experimental evidence is not available to indicate how much individual experience may affect this behavior. Might such an egg-laying female think consciously about what she is doing? She will die long before her offspring emerge, so that she has no direct information about the eventual result of her complex efforts, although she did of course begin life as a larva in a similar nest. While a female *Osmia* may have no possibility of understanding the long-term advantages of her elaborate efforts, she might nevertheless think consciously about the immediate present or very short-term future. She might strive to close the snail shell after laying eggs and feel good about hiding it, even though she has no understanding that offspring will eventually emerge.

Other wasps dig tunnels in the ground or into solid wood and lay eggs in them. The tunnel opening is then plugged, and some species select material for the plug that matches the surroundings so well that the burrow opening is very difficult to detect. In the sand wasps (*Amphiphila campestris*) studied by Baerends (1941) the burrows are dug in sandy ground with an enlarged chamber at the lower end. These wasps close the opening with small stones, which they bring from some distance if none are available in the immediate vicinity. Then the wasp searches for and captures a caterpillar, which ordinarily is as large as herself. She paralyzes it by stinging it in several places and carries it on the wing to the burrow. There she opens the entrance, drags the caterpillar down to the nest chamber and only then lays an egg. Paralyzed caterpillars survive well enough that the growing larvae can eat them.

As reviewed by Thorpe (1963) and described in detail by van Iersel and van dem Assem (1964), the sealing of wasp burrows is accomplished very skillfully, so that after it is completed it is virtually impossible to see any signs of disturbance. When digging a burrow, the wasp throws sand grains some distance away so that they do not create a revealing pile of material. The female, on returning with a caterpillar, re-

locates her hidden burrow by remembering the appearance of surrounding landmarks. If these are experimentally altered she may be unable to find the concealed burrow entrance.

This type of complex burrow construction and provisioning has been studied experimentally by intervening in the process in ways that would not normally occur. For example if a paralyzed caterpillar is moved after the wasp has dropped it near the burrow entrance while reopening the hole, she hunts about for the missing prey and drags it back to the entrance. But in many experiments she then repeats the entire behavior of depositing the caterpillar near the entrance and digging even though the burrow has already been opened. This has often been taken as evidence that the entire pattern is rigidly programmed genetically, and the further assumption is customarily added that for this reason the wasp cannot possibly think consciously about what she is doing. Similar examples have received a great deal of emphasis. When some insects have constructed a nest they may fail to alter their behavior if an experimenter opens a hole in the wall or bottom of the nest so that the eggs fall out as soon as they are laid. We can immediately see what the insect ought to do to accomplish her general objective; and when she fails to do this, and instead repeats what would ordinarily be appropriate behavior in this abnormal situation, we tend to conclude that she is a mindless robot. But in other cases insects do behave sensibly and repair damaged nests. Undue emphasis has been placed by inclusive behaviorists on the examples of stupid behavior, and because many insects often fail to adjust their behavior after abnormal experimental disturbances, we have overgeneralized such inefficient behavior into a dogmatic conclusion that no insect ever thinks consciously about its activities.

The leaf-cutter ants of the genus *Atta* are in many ways one of the most successful species in the world if judged by the number of well-nourished individuals and their impact on the immediate environment. The general behavior of these ants has been well reviewed by Weber (1972) and by Hölldobler and Wilson (1990). They live in enormous underground colonies consisting of many chambers interconnected by tunnels. Each colony is founded by a single queen, but she lays eggs that develop into thousands of nonreproductive workers. Males and virgin queens are produced only after such a colony has grown to a substantial size. The workers are adapted both in anatomy and behavior for different functions such as caring for eggs, larvae, and pupae, gathering food, or defending the colony against intruding insects of other species as well as against vertebrate predators. The food-gathering workers move out

from the entrance over the forest floor in such enormous numbers that they quickly wear down the vegetation and form beaten paths. They climb plants of all sizes, cut pieces of leaf roughly the size of their own bodies, and carry these back to the colony. Often they can be seen by the hundreds walking methodically along their trails, each ant carrying a tiny green fragment. When they attack flower beds, the dismayed gardener may be startled by a busy trail of five-millimeter fragments of colorful flower petals being carried to the underground tunnel system.

Inside the colony the workers carry leaves or flower petals into special chambers containing masses of fungus. These chambers may be as large as a meter in diameter, and the fungus grows rapidly, nourished by the leaf fragments as well as by feces of the ants. The leaf cutters, like certain other species of ants, are in a very real sense engaging in a form of agriculture. They collect particular food plants, bring them into the colony, and manipulate the fungus in appropriate ways to facilitate its growth and the processing of the food, which the ants themselves could not digest unaided. In addition to gathering food and tending the fungus "gardens," the ants devote much effort to caring for eggs and larvae. While much of the behavior of leaf-cutter ants is relatively predictable, the workers vary their activities according to the needs of the colony to some degree. It has not been practicable to rear such ants in isolation in a way that would serve to tease apart the relative contribution of genetic constructions and individual experience, but, as in so many other cases of complex animal behavior, it would seem that a little elementary conscious thinking would be helpful. For example, when suitable food has not been found in one area, the leaf-cutter ants shift their foraging activity to other places. They certainly exploit newly available food sources by massive invasions that can be totally destructive to human gardening efforts.

Another group of specialized ants, the African weaver ants (*Oecophylla longinoda*), exemplify the capabilities of millimeter-sized central nervous systems (Hölldobler and Wilson 1990). Weaver ants live primarily in trees, but instead of digging a burrow or nesting cavity they construct nests by joining together leaves. The edges of the leaves are attached with sticky silk, to form closed chambers considerably larger than the bodies of the ants that build them. Nest construction is carried out by nonreproductive female workers, like most of the activities of social insects. The first problem in constructing a nest is to bend leaves out of their normal flat shapes and join the edges to form the walls of an enclosed cavity. Sometimes one ant can grasp one leaf with her rear legs and the other with her jaws and by bending her whole body and flexing

her legs can pull the edges of the leaves together. But since the individual ants are much smaller than the leaves, numerous workers must line up along the edges of two leaves and all pull in a roughly coordinated fashion. Even this degree of cooperation is not sufficient when the leaves are separated by more than an ant's body length. This problem is solved by the ants forming chains, one seizing the edge of a leaf in her jaws, another holding her by the abdomen, while a third holds that ant's abdomen, and so on until at the end of a chain of several ants one grasps the second leaf with her hind legs. Numerous chains of ants pulling and bending leaves in rough coordination form them into an enclosure that will later be occupied as a nest.

This shaping of leaves and bringing their edges together by the cooperation of numerous individual weaver ants is only part of the process. Once brought together, the edges of leaves must be joined with silk. But the adult workers cannot secrete this silk themselves. It is obtained by carrying larvae of appropriate age from another nest and holding them first against one leaf edge and then the other. Thus the younger sisters of the workers are used as a sort of living tool in nest construction.

The queen weaver ant lays her eggs, and larvae grow and are fed by workers that bring food into these nests. The food consists mostly of fragments of other animals the foraging workers have killed or scavenged. But one leaf nest is seldom large enough to hold a growing colony, so that while the queen remains in the first nest the workers construct others nearby and then carry food, eggs, and larvae back and forth between them. Sometimes these colonies grow to consist of dozens of nests extending over several trees.

All this social behavior, which is necessary for the survival and reproduction of the colony, would seem to be facilitated if the workers were capable of simple conscious thinking. When starting nest construction they might intentionally work to pull the edges of leaves closer together. When leaves have been bent into approximately an appropriate shape, some workers might consciously realize that it is now necessary to glue them together and fetch larvae of a suitable age to secrete the necessary silk. Coordination of this building activity must require some sharing of information about what needs to be done. But this is probably carried out in large measure by chemical signals which are very difficult to analyze. In the case of food gathering, however, communicative behavior of weaver ants and other species has been studied in sufficient detail that we can understand at least the basic processes by which cooperative endeavors are coordinated, as will be discussed in chapter 9.

## Bird Nests

The nests of birds are larger and more familiar to us than those of insects, but when one takes into consideration the difference in size of the builders many bird nests appear rather small and simple compared to the elaborate structures built by some of the social insects. Yet other bird nests, such as those of orioles, are covered structures with long entrance tubes. The elaborate nests of African weaver birds have been studied extensively by Collias and Collias (1962, 1964, 1984) and by Crook (1964); these and other complex bird nests are also described by von Frisch (1974) and Hansell (1984). The nest of the village weaver (*Textor* or *Ploceus cucullatus*) of Africa is an ingeniously complex woven structure, and the detailed observations and experiments of Collias and Collias have provided a more complete understanding of how it is built than is available for other species.

The finished nest of the village weaver is a roughly spherical structure with an opening leading downward from one side of the bottom. The nest is constructed from strips of grass or similar material, which are woven by a series of fairly complex motions. When courting a female, the male weaver begins nest building by forming a roughly vertical ring attached at two or three places to a small branch. The ring is then enlarged at the top forming first a partial roof and later the walls of a roughly spherical chamber. The entrance is completed last. The actual building operation consists of grasping a strip of grass near one end and poking it with a vibratory motion, at first alongside some object such as a twig, and later into the mass of previously placed strips. When the end of the strip sticks in place, the bird releases its grip, moves to the other side of the twig or nest mass, and seizes the strip again with its bill. It then pulls it through or around whatever material is already present, bends or winds it about the original twig or another piece of nest material and finally pokes the end of the strip back into the accumulating mass. A constant feature of the stitching process is that, with successive pokings of the strip, the bird reverses the direction in which it is wound around some preexisting object. Different parts of the nest receive different amounts and kinds of material, so that the end result is a structure with a virtually waterproof roof, thicker than the walls, and a short, roughly cylindrical entrance tube. When a female accepts the male's courtship displays, and the nest he has constructed, she adds a soft, thick lining at the bottom of the egg chamber, first covering it with a thin layer of strips that she tears from leaves of tall grasses or palm fronds. After accomplishing this task, she inserts many soft grass tops with the



stem end down, so that their feathery tops provide a soft cup. When feathers are available the female gradually begins to use them until there is a thick layer of feathers on top of the grass heads.

The tailor bird (*Orthotomus sutorius*) of India constructs its nest by stitching together leaves to form a protective cup. Plant fibers or spider silk are used as threads, and these are sometimes threaded through holes made by the bird at the edge of the leaves. While many species of birds construct their nests by a variety of motor actions that serve to produce a structure that is sturdy, and often is camouflaged to make it less conspicuous, the weaving and stitching procedures are especially suggestive of conscious thinking about the process and its results.

It is customary to view nest building by birds as genetically programmed behavior. In some species such as canaries, which build relatively simple cup-shaped nests, naive females that have never seen a nest do construct a reasonably normal one when ready to lay eggs. But in the case of the village weavers a considerable amount of learning seems to be involved. Young males build partial and irregular nests, but these are not accepted by females. Their nest building skill is increased if they can watch adult males building nests. Thus the male that builds the relatively complex structures has ordinarily had a long period of practice and has also had abundant opportunity to watch older males build more complete nests. While the general pattern of a village weaver nest is fairly constant, each male adapts his building efforts to the immediate situation, especially to the shape and position of the twigs where he starts nest building.

Birds generally repair damaged nests in a reasonably sensible fashion and do not go through the entire sequence of building unnecessarily. When Collias and Collias removed parts of a nearly completed weaver bird nest, the male rebuilt those parts and did not go through wasteful repetitions of other portions of the building sequence. The only partial exception to this rule involved the entrance tube. If this was damaged, the male generally built an abnormally long tube.

Nesting birds behave in many appropriate and rational ways when raising young. Even simple nests are often concealed in vegetation, that is, are constructed in places where they are difficult to see. Furthermore the parents arrive and depart from their nests quietly and inconspicuously. This is obviously advantageous, because many predators eat eggs and young, and either the nest or the arriving and departing parent are obvious signs that food is available.

This is not to say that birds never do foolish things in the course of nest building. Von Frisch (1974) describes how blackbirds occasionally

start building many nests in some artificial structure that has many similar-looking cavities. The birds apparently become confused as to just where the nest is to be and never succeed in completing any one nest. As in so many cases of this kind, we tend to infer a total lack of thinking when animals do something foolish and wasteful of effort. But we do not apply the same standard to members of our own species, and we never infer a total absence of thinking when people behave with comparable foolishness. It is important to realize that to postulate that an animal may engage in conscious thinking is by no means the same as to say that it is infinitely wise and clever. Human thinking is often misguided, and there is no reason to suppose that animal thinking always corresponds perfectly to external reality. Our thoughts may be inaccurate or quite different from what others see as correct and sensible. But error is not the same as absence of thought.

Events in our own lives show that stupidity does not preclude consciousness. If our usually dependable automobile fails to start, in our impatience many of us do something totally irrational, such as kicking the tires or swearing at the machine. We know perfectly well that such displaced aggression will not start the car, but we are probably thinking, "Why won't the damned bus start this morning?" or "What will happen when I am late at the office?" or "I should have bought a new battery last fall."

This leads us to another challenging question about nest building and other complex reproductive behavior of birds. When they are at an early stage of nest building, do birds have any concept of the finished product they are working to achieve? We might go one step further and ask whether a bird beginning to build a nest has any idea of the eggs and young that will soon occupy the nest. Such speculation may be more plausible in species where the females do the nest building, for they will lay the eggs and feed the young. Many will feel that it is outrageously far-fetched to suggest that a female bird might think about eggs and young as she begins to build a nest, but there might be some advantages to such thoughts. Even a simple concept of the function the nest will serve could help birds construct it appropriately. But again we are stymied by our inability to gather convincing evidence.

What can we say about the possible conscious thoughts and feelings of nest-building birds? The conventional assumptions of inclusive behaviorists has been that nest building is a complex but predetermined form of behavior. The predetermination may stem from genetic information or learning; ordinarily some mixture of the two. One clear example of genetic influence on nest-building behavior stems from the

experiments of Dilger (1960, 1962) with two species of lovebirds of the genus *Agapornis* which hybridize in captivity. One, *A. personata fischeri*, builds its nest from pieces of bark that it carries in its beak. Another, *A. roseicollis*, cuts strips of nest material from vegetation, which it carries by tucking them into feathers on its back before flying to the nest. In the experiments, hybrid birds cut paper strips but were inefficient in transporting them, apparently attempting both to tuck strips and to carry them in the bill. They improved with practice, however, and most ended by carrying strips in the bill after initial and incomplete tucking movements. This is a classic example of behavioral genetics where there is clearly a strong inherited tendency to behave in a certain way and yet the animal does not follow the genetic instructions slavishly but gradually modifies its actions on the basis of experience and succeeds in obtaining an apparently desired and intended result.

Despite the lack of completely conclusive evidence, it seems plausible that nest-building birds have some simple conscious desire and intention to produce an appropriate structure. Genetic influences may determine the general pattern of the desired result, but birds certainly vary their behavior as they work to achieve this goal. Although their efforts are not always totally efficient, and human observers can often imagine how they might do somewhat better, the birds give every indication of trying to achieve an anticipated goal.

### Bowerbird Bowers

In many ways the most impressive structures built by any animals are the bowers constructed by male bowerbirds of Australia and New Guinea. Displaying males attract females to these structures, and mating takes place in them. Darwin placed considerable emphasis on the bowerbirds in his discussion of sexual selection, and more recent investigators have discovered many important facts about their behavior. The Australian biologist Marshall (1954) described and analyzed the behavior of bowerbirds in great detail, emphasizing physiological and endocrine influences on their courtship displays and bower building. Gilliard (1969) pointed out that among bowerbirds and their relatives there is an inverse correlation between striking plumage and elaborate bowers. Species with conspicuous colored feathers used in courtship displays build simple bowers, if any, while the most elaborate bowers are constructed by species with relatively dull plumage. More recently intensive studies of individually marked birds has added new dimensions to our understanding of their social behavior, beginning with the observations

of Vellenga (1970, 1980) and Warham (1962), and continuing with increasingly ingenious methods in the studies of Borgia (1985a, 1985b, 1986), Borgia, Kaatz, and Condit (1987), and especially Diamond (1982, 1986a, 1986b, 1987, 1988).

Fourteen of the eighteen species of bowerbirds build bowers or at least make small clearings on the ground, which they decorate to some extent. Bower style varies with the species. It is convenient to begin with the relatively simple avenue bower built by the satin bowerbird (*Prilomorhynchus violaceus*). Adult males are glossy bluish-purple and the females and immature males are green. This species has been more thoroughly studied than any other because it is common in eastern Australia and sometimes builds its bowers in suburban areas where it can be observed more easily than its relatives that are found only on uninhabited mountains of New Guinea. Vellenga (1970, 1980) took advantage of this opportunity by color banding 940 satin bowerbirds captured in her garden over a period of five years. One of these individually identified birds could be traced to a park half a mile away where he maintained and defended his bower for fifteen years. Her observations of known individuals confirmed several aspects of bowerbird behavior that had previously been inferred by Marshall and others on the basis of less direct evidence.

As summarized by Diamond (1982, 99–100), largely on the basis of Vellenga's observations:

The bower is a woven platform about 10 feet square, supporting an avenue of woven sticks, with walls a foot high nearly joining in an arch over a floor, and decorated with blue or green natural or man-made objects. Perishable decorations such as flowers are replaced daily. Some bowers are left unpainted, but others are painted daily either blue, black, or green by the male, using a wad of bark as a paint brush and using crushed fruit, charcoal, or (nowadays near civilization) stolen blue laundry powder as paint. The long axis of the bower is generally within 30 degrees of north-south, possibly so that the male and female can face each other during early morning displays without either having to stare into the rising sun. When Marshall picked up a bower and reoriented it, its architect promptly demolished it and rebuilt it in the correct orientation. . . . The bower-owning male Satin Bowerbird continually tries to entice females into his bower by picking up in his bill an object such as a flower or snail shell, and posturing, dancing and displaying to the female.

The males also call loudly. As described by Borgia (1986, 98) the male "faces the female while he stands on the platform. He gives a whirring call while prancing, fluffing up his feathers and flapping his wings to the beat of the call. Calls are punctuated with periods of silence, quiet

chortling, buzzing, or mimicry of other birds. The female's initial response is to enter the bower and 'taste,' or nip, at a few sticks. Then she intently watches the courtship. If she is ready to copulate, she crouches and tilts forward." Diamond (1982, 100) emphasizes the fact that

many courtships are interrupted at a crucial stage by the intrusion of other individuals. However, another reason for the low success rate may be the invariant sequel to successful mating: the male bowerbird savagely attacks the female, pecks and claws her, and chases her from the bower. Mating itself is so violent that often the bower is partly wrecked, and the exhausted female can scarcely crawl away. The courtship display can appear little different from the male's aggressive display. When a courted female is won over and starts to solicit copulation, the male often changes his mind and chases her away. Thus, a female may have to make many visits to a bower before she overcomes her fear of the aggressive male. After mating, the female constructs a nest at least 200 yards from the bower and bears sole responsibility for feeding the young.

Bowers, like flags of possession, may serve as symbols of males' property rights in their wars with other males. An adult male spends much time repairing his own bower, protecting it from raids by rivals, and attempting to steal ornaments or destroy rivals' bowers. The battles and territorial shifts that Vellenga recorded among her 426 banded adult males make the European Thirty Years' War seem straightforward by comparison. . . . Dominant males directly prevent other males from wooing females by the destruction of their bowers. Young males continually try to erect rudimentary bowers in the territory of an adult male but the latter patrols his property several times a day and wrecks them. When Marshall placed 100 pieces of numbered blue glass into these rudimentary bowers one night he found 76 of the pieces transferred to the bowers of dominant males by noon the next day. Similarly, Vellenga observed a blue celluloid band to be transferred between bowers several times a day, until one male firmly wove it into his bower.

Borgia (1985a) and several collaborators observed the mating success of many individually marked male and female satin bowerbirds, using an automatic recording camera to monitor 207 copulations at 28 bowers during one season. The number of copulations at each bower varied from zero to 33, with five of the 28 males achieving 56 percent of the matings. There was also a statistically significant tendency for males with well-constructed and highly decorated bowers to mate with more females. The most attractive bowers were more symmetrical, included larger sticks more densely packed, and were decorated with more blue feathers, yellow leaves, and snail shells. In another investigation of flower preferences Borgia et al. (1987) found that male satin bowerbirds selected primarily blue and purple flowers and never used those

that were orange, pink, or red. Furthermore they showed a preference for blue and purple flowers that were uncommon in the local environment.

Borgia (1985b) also studied the effects on mating success of bower destruction by other males. He found that the number of destructive attacks on bowers, and the amount of destruction, were inversely correlated with the quality of the bowers, that is, their symmetry, size of sticks used, density of stick packing, and general quality of the bower as judged by the investigators. Bower destruction occurred only when the bower owner was absent, ordinarily to feed, and on his return the owner almost always drove off the raider. Since bower quality had been shown to be correlated with mating success, it is clear that the competitive bower raiding has a direct effect on the evolutionary fitness of the males. In addition to partial or complete wrecking of bowers, neighboring males often steal feathers and other decorations to improve their own bowers (Borgia and Gore 1986).

All this complex interaction of competing males using elaborate bowers to attract females suggests that some simple conscious thinking may be involved when bowers are being constructed or decorations gathered and set in place. Advocates of the "sleepwalker" view of animal behavior may be tempted to argue that because all this behavior has such an obvious effect on the birds' evolutionary fitness it must be genetically fixed and therefore mindless. But as has been found to be the case with many behavior patterns, the generally similar actions performed by members of the same species do not preclude a major role for individual experience and learning. Early in the mating season, as summarized by Borgia (1986), "young males visit the bowers and the bower owners often display to them . . . [but later] the bower owners become less tolerant of male visitors." Vellenga's earlier studies had shown, as summarized by Diamond (1982, 101), that

many skills related to bower building and use have to be learned. Young males in green plumage spend about two years building rudimentary but increasingly complex bowers before acquiring blue adult plumage and building complete bowers. These "practice bowers" are the joint efforts of several young males, which take turns placing and rearranging sticks, often clumsily and without success, occasionally with the cooperation of more skilled older males. The young males do not paint these bowers and are less discriminating than adult males in choice of colour for bower decorations. The young males spend much time watching the displays, mating and other bower activities of adult males, and are displayed to by adult males.

Other species of bowerbirds build quite different types of bowers, but all seem to serve the same basic function of attracting females. For example, the stagemaker or tooth-billed bowerbird (*Scenopoeetes denti-rostris*) of North Queensland clears a roughly circular area of the forest floor. As described by Gilliard (1969, 276), largely from the observations of Warham (1962) and Marshall (1954),

the male clears all the fallen debris from this space of earth as if with a broom. He then decorates it with fresh green tree leaves of one or more favoured species . . . the leaves may be up to twice as long as the male which carries them to his bower. These leaves are almost always placed upside down on the "meticulously clean" court and are replaced with fresh leaves when they wither. The tooth-edged bill (for which the bird is named) serves as a specially modified tool for severing fresh leaves. . . . At one bower Warham found 56 leaves. He removed all of them . . . [after which] almost every day the male carried in from 2 to 10 leaves and placed them carefully on the ground court.

Within a week 25 leaves had been gathered to replace those that had been removed.

Archbold's bowerbird of the New Guinea highlands (*Archiboldia papuensis*) makes a display ground of flattened ferns and other vegetation but decorates it with piles of snail shells and sometimes black beetle wing covers. MacGregor's bowerbird (*Amblyornis macgregoriae*), also found in the New Guinea highlands, clears a roughly circular area and forms at its center a "maypole" consisting of "a column of sticks erected around a thin sapling" (Gilliard 1969). Moss is gathered and placed on the cleared area around this vertical pile, which may be as much as a meter in height. The golden bowerbird (*Prionodura newtoniana*) of Queensland constructs a double column of sticks, each somewhat like the "maypole" of MacGregor's bowerbird but with a roughly horizontal stick connecting them. The male perches on this stick during parts of his displays. All of these styles of bower construction show considerable variation from place to place and from one individual to another, indicating that they are not fixed, stereotyped building behavior patterns.

Perhaps the most impressive of all bowers are some of those constructed by certain populations of the Vogelkop gardener bowerbird (*Amblyornis inornatus*). These have been studied by Diamond (1982, 1986b, 1987, 1988), who not only has described how they vary between populations of the same species, but has demonstrated by ingenious experiments how the birds select decorations of preferred colors. These birds are confined to rugged, uninhabited mountains of western New Guinea which are very difficult to reach because of both physical

and political obstacles. In the Wandamen Mountains the bowers are truly impressive huts 40 to 80 cm high and from 90 to 220 cm in diameter formed by weaving sticks together. On the downhill side of the hut is an opening 18–58 cm wide and 20–28 cm high. As described by Diamond (1987, 189), “the hut was built around a sapling at whose base was a green moss cone 20–23 cm in diameter and 15 cm high, with a low stick tower joining the cone to the ceiling of the hut. The hut rested on a green moss mat.”

In the Kumawa Mountains, about 200 km from the Wandamen range, the same species builds much simpler bowers, which lack any roofed hut but consist of maypoles, moss mats, moss cones, and stick towers similar to those located inside the huts of the Wandamen birds. In both cases small, conspicuous decorations are added by the birds. The moss mats are “woven tightly from fine, clean, dry, dead fibers of a moss that grows abundantly on trees” (Diamond 1987, 182). These mats at some bowers were almost perfect circles; when the diameter was measured across the circle in several directions it varied by only a few percent. The “maypoles” were saplings 1 to 3 cm in diameter without leaves or branches up to 1.5 to 4 meters above the ground. The moss cones were formed from the same moss used to make the mat. Stick towers consisted of hundreds of 20 to 90 cm sticks piled against each maypole. Around the base of the tower the sticks lay horizontally, radiating neatly in all directions. In both areas there was also some variation in size and details of construction between individual bowers.

Most of the Kumawa bowers were decorated with dead pandanus leaves 20 to 150 cm long, often leaning against the maypole sapling. Some of these leaves weighed half as much as the bird, who must have dragged them for many meters from the nearest pandanus tree. Other common decorations were the brown shells of land snails, dark brown acorns, brown stones, beetle elytrae, and piles of 22 to 90 brownish sticks 8 to 100 cm in length. The Wandamen bowers were decorated quite differently. Most common were 20 to 50 cm piles of black bracket fungi or groups of 4 to 32 dark brown or blackish beetle elytrae. Red and orange fruits were also present at most bowers, along with red leaves and black fungi other than bracket fungi, plus black fruits. Particular decorations were preferentially placed in certain areas relative to the bower, for instance black and orange bracket fungi downhill from the door. Colored flowers, red leaves, red, orange, or green fruits were usually outside the bower on the mat, and objects chosen infrequently as decorations were usually inside the hut. These rare items included butterflies, beetle heads, amber beetles, acorns, and orange pieces of bark



or jellylike fungus. In some cases decorations of the same color were grouped more or less together. When Diamond altered these arrangements by shifting decorations to atypical locations the birds usually put them back where they apparently belonged.

All of these observations suggest that individual Wandamen bowerbirds were expressing preferences for certain patterns of decoration. Given the fact that young male bowerbirds practice bower building and watch experienced adult males building bowers and courting females at them, it seems likely that these local and individual preferences in decorating bowers are learned manifestations of what Diamond (1986b, 3042) calls a "culturally transmitted trait, like human art styles." To test this interpretation Diamond (1988) placed poker chips of seven bright colors in or near the bowers of both Kumawa and Wandamen bowerbirds. In the Kumawa area, where the birds do not naturally use colored objects to decorate their bowers, most males removed the poker chips placed in their display areas, and did not bring any in from nearby. At Wandamen bowers, however, the birds gathered many poker chips and arranged them in their bowers, showing a hierarchy of preferences with blue collected in largest numbers, followed by purple, orange, red, lavender, yellow, and white in that order. But these relations differed among individual birds, and whichever color was preferred was gathered first, stolen from other bowers first, and removed from the bower least often. Poker chips of the same color tended to be grouped close to each other, and also close to natural objects of similar color. Two or three poker chips of the same color were sometimes stacked on top of each other; occasionally a chip of a preferred color was piled on top of a less favored color. In general poker chips were treated in much the same ways as naturally occurring decorations.

This panoply of construction and decoration strongly suggests that the bird is consciously thinking about what it is building. Of course, determined behaviorists can always dream up complex sets of genetic instructions that might operate to generate whatever behavior may be discovered. In the case of bowerbirds, this exercise will require more ingenuity than in many other cases. If we allow ourselves to speculate as to what these birds might be thinking as they work at their bowers, the goal of luring a female ready for mating may well be prominent in the content of their thoughts. Marshall (1954) and others have argued that because bower building and decorating are so clearly part of the birds' reproductive behavior, they were not accompanied or influenced by aesthetic feelings. Yet toward the end of his monograph, which emphasized the hormonal control of bowerbird reproduction and the behavior ac-

companying it, Marshall recognized that the birds may well enjoy the bowers they build. As von Frisch (1974) pointed out in his book *Animal Architecture*, it would be difficult to deny that impressing females motivates much human artistic creation. Unless committed a priori to an absolute human/animal dichotomy, we have no basis for rejecting out of hand the hypothesis that a male bowerbird thinks in simple terms about the bower he is building and decorating, the other males competing with him, and the females he hopes to entice for mating.

### Beaver Engineering

When we consider the kinds of animal behavior that suggest conscious thinking, the beaver comes naturally to mind. These large aquatic rodents manipulate their environment in rather spectacular ways to obtain food and shelter. They fell trees and construct conspicuous lodges as well as digging less obvious bank burrows. They also deepen shallow stretches of water to form channels where they can swim and tow branches that would otherwise drag on the bottom. Beaver carry mud dug up from the bottoms of these channels to piles that may form small islands. This behavior may extend to digging canals through dry land that are also used to float branches to food storage piles. These canals and channels are not dug helter-skelter but along routes the beaver use to travel between a lodge or burrow and food supplies. Finally, as everyone knows, some beaver create ponds by building dams across small streams. While they are far from being perfectly efficient engineers, their activities have a more obvious and substantial impact on their surroundings than those of most other mammals.

This review of beaver behavior is based primarily on the detailed studies of Morgan (1868), Wilsson (1971), Richard (1960a, 1960b, 1967, 1980, 1983), Hodgdon (1978), Patenaude (1983), Patenaude and Bovet (1983, 1984), and Ryden (1989). Wilsson and Richard studied captive beaver for the most part, while Hodgdon and Ryden concentrated on extensive observations of wild beaver under natural conditions. Patenaude succeeded in arranging an observation window that permitted video taping of beaver behavior inside the lodge.

Beaver typically live in family units consisting of a monogamous pair of adults and their young. One litter of three or four kits are born each spring, and they usually stay with their parents for two years. The yearlings help by feeding and grooming their younger siblings, and some stay with their parents for a third year (Hodgdon 1978). Although the adults do more dam and lodge building than their offspring, the year-

lings participate to some extent. Many aspects of beaver behavior seem to vary from one situation or population to another, so that there are no absolutely fixed patterns of behavior that occur under all natural conditions. Scientists concerned with animal behavior have paid relatively little attention to beaver despite the impressive scale and scope of beaver works. One reason is the difficulty of observing a largely nocturnal animal that spends much of its time out of sight in a lodge or burrow. Furthermore, most of its body is submerged a great deal of the time, and some of its most interesting behavior occurs underwater or even under the ice in midwinter.

As emphasized by Richard (1960b, 1967, 1980, 1983), it is difficult to repress the inference that beaver could scarcely accomplish what they do without some awareness of the likely results of their activities. He studied captive beaver in a fenced "Parc à Castors" about  $180 \times 60$  meters in size with a small stream flowing through it. They built dams and lodges, and Richard was able to observe many details of their behavior and to perform experiments that tested their ability to solve problems quite different from the normal experience of their species. Some individual beaver learned to open puzzle boxes to obtain food, even when this required manipulating different types of latch. When confronted with food out of reach on a small platform at the top of a one-meter pole, some beaver piled branches around the pole until they could climb up this pile to reach the food.

Richard's Parc à Castors contained numerous willows on which the beaver were free to feed, except for a few trees that were declared off limits "as in the Garden of Eden" to preserve the appearance of the park and to provide shade. These trees were protected by a cylindrical fence of heavy netting firmly anchored in the ground and wired securely to branches above the beavers' reach. But the beaver solved this problem by piling a pyramid of branches and mud around the tree, and climbing up this pile to reach the unprotected trunk, which they then cut in their usual fashion. They did this to similarly protected trees on several different occasions.

Pilleri (1983, 99) reports an ingenious response to a novel situation by two beaver confined in an enclosure where the water level of a  $3.5 \times 2.5$  meter pool 1.6 meters deep was regulated by an outlet pipe equipped with a cap perforated by three holes 8 mm in diameter through which the water escaped. After about two weeks the two beaver began to plug these three holes with "peeled twigs which had been gnawed off obliquely at both ends by the beavers and whittled down in such a way that they exactly fitted the holes. . . . The performance was

repeated several times, always at night, after we had removed the sticks in the morning and restored the water in the pool to its normal level. Every night the beavers made new calibrated sticks and blocked up the holes. . . . [Finally they] changed their technique. In addition to the sticks they used grass and whole piles of leaves mixed with mud."

Many scientists disagree with Richard's conclusion that beaver know what they are doing, claiming that all their construction of burrows, lodges, canals, and dams result from genetically programmed action patterns that involve no conscious thinking or anticipation of the results of these activities. For example, after one of the most thorough studies of beaver behavior involving both free and captive animals, Wilsson (1971, 240–54) concluded that even those actions that seem most intelligent can be explained as the result of genetically programmed motor patterns. He specifically disputes the conclusion reached by Richard (1967) that beaver exhibit some degree of forecasting and "unformulated thought."

The examples he [Richard] gives as evidence for "forecasting," "intelligence" and "some kind of unformulated thought" can . . . just as well be interpreted as stereotyped phylogenetically adapted reactions. For example, the fact that a beaver often thoroughly investigates a leak in the dam, then leaves it for some hours and later brings different kinds of material with it when it returns to repair it, does not necessarily mean that it is able "to forecast in the choice he makes of building materials which depends on the use made of them as well as the shape his construction will take." . . . Dam building behaviour is activated when the animal has received stimuli from the dam for a certain time and a delayed response is not unusual in phylogenetically adapted behaviour. (Wilsson 1971, 247)

Yet, despite this insistence that their behavior is stereotyped, Wilsson (1971, 187–89) describes how some of his captive beaver first piled material at a water outlet, but when this did not raise the water level in their tank, they changed their tactics to a more appropriate placing of sticks and mud at the inlet. Thus, as pointed out by Richard (1983), dam building behavior is sometimes modified as the beaver learns that one placement of material is ineffective in raising the water level.

A vivid recent example of the strong tendency to deny conscious intent has recently been expressed by the anthropologist Ingold (1988, 86, 90). He points out that one of the earliest scientific studies of beaver engineering was conducted by Lewis Henry Morgan (1868), who was also, in Ingold's words, "one of the founders of the discipline of anthropology as we know it today." After quoting Morgan's opinion that bea-

ver fell trees and build dams with at least some rudimentary anticipation of the results of their activities, Ingold vigorously denies the correctness of any such inference. He cites approvingly the assertion by the American anthropologist Kroeber (1952) that (in Ingold's words) "the beaver *does not* and *cannot* construct an imaginary blueprint of his future accommodation, whereas this is something of which even the most 'primitive' human is capable [italics are Ingold's]. The human engineer constructs a plan in advance of its execution; the beaver lives merely to execute plans designed—in the absence of a designer—through the play of variation under natural selection." In all fairness to Kroeber, it should be mentioned that he expressed this view originally in 1917, long before ethologists discovered how versatile animal behavior can be.

Ingold goes on to support his assertions by appealing to the authority of Karl Marx: "What from the very first distinguishes the most incompetent architect from the best of bees, is that the architect has built a cell in his head before he constructs it in wax." Proving a global negative statement, that something never happens under any circumstances, is notoriously difficult; but Ingold and others deny that beaver might be aware of the results of their actions, without presenting any convincing evidence to support such a sweeping and dogmatic assertion.

Ingold reiterates his conviction that "*animals have no thoughts,*" and, "rather than thinking without communicating, the animal *communicates without thinking*; so that the signals it transmits correspond to bodily states and not to concepts" (94 and 95; italics are Ingold's). It is difficult to reconcile this vehemently negative assertion with the evidence I shall be reviewing in later chapters, especially the experiments showing that pigeons can be taught something closely resembling concepts. Yet in a section titled "Thinking, feeling and intending," Ingold recognizes that animals are probably conscious of "doing and feeling." "Morgan in his time, and Griffin in ours, are suggesting that . . . beavers . . . plan things out, or envisage ends in advance of their realization. I do not think they do; but more than that, I do not think human beings do either, except intermittently, on those occasions when a novel situation demands a response that cannot be met from the existing stock-in-trade of habitual behavior patterns" (95–97). No one has ever suggested that animals *always* think consciously about what they are doing or the likely results of their activities (although on page 96 Ingold accuses me of that absurd claim, a typical example of discredit by exaggeration). What is so puzzling is how Ingold and others can recognize the likelihood that animals are sometimes, even if only rarely, conscious of what they are

doing, yet feel so strongly committed to denying that animals are capable of any foresight, even for a short time into the future, or any thoughts about the likely results of their own activities.

Given this basic uncertainty and disagreement, can we throw any light on these questions by considering the actual behavior of beaver? A good place to begin is their digging of burrows and construction of lodges. Under natural conditions most beaver dig burrows into the banks of whatever streams or lakes they occupy. Burrows start underwater, and then turn upward until it becomes possible to construct a reasonably dry chamber. Beaver seldom if ever start digging burrows where the ground slopes too gradually to provide space for a beaver-sized tunnel above the water level. This implies that they recognize that some shores are too low to make burrowing worthwhile. As far as I have been able to learn from published accounts of beaver behavior or from my own observations, beaver do not start useless burrows. But aborted burrows would be difficult to locate, so that lack of reports of their occurrence is not conclusive evidence of their absence. Perhaps they make this selection on the basis of steep underwater banks, but it seems more probable, pending appropriate investigation of the question, that beaver explore shorelines and select for burrowing only places where the ground rises far enough to provide space for a dry chamber within a reasonable distance of the water.

Burrow construction by beaver and other animals is an interesting sort of goal-directed behavior. It may even be directed toward the consciously perceived goal of providing a dry shelter. But the fact that burrowing occurs underground and sometimes also underwater greatly restricts the sort of observational or experimental evidence that can be obtained without difficult and costly special procedures. Animals can be observed starting to dig a burrow, and completed burrows can be excavated and mapped; but the actual behavior of digging them, deciding in what direction to progress, and coping with obstacles such as rocks or tree roots remains almost totally unstudied.

When beaver burrows begun under water turn upwards as they progress under and beyond the shoreline they often reach the surface and break through to the air. Beaver sometimes pile sticks and mud over this opening and continue burrowing upward through the material they have added. Since their teeth can easily cut branches and shred woody material into soft bedding, they can burrow from below into a pile of their own making at least as easily as through a natural bank, where the earth is often studded with roots and stones. This addition of new material may occur either after an actual opening to the air or shortly be-

forehand. As with many other aspects of beaver behavior, different populations seem to differ in this respect. But in either case the beaver brings mud and branches from some distance to a spot on the shore where its burrow is close to opening, or has already opened to the air.

Bank lodges formed by adding material above a burrow often become island lodges when the construction of a dam raises the level of the water. But some island lodges are also built a short distance from the shore of lakes where the beaver build no dams and where the water level does not fluctuate appreciably. Hodgdon (1978) observed cases in which the beaver started an underwater burrow at a place where the water's depth varied steeply although all the immediate area was under water. When the burrow broke through the earth, still below the water surface, they piled branches and mud over the opening and thus created an island lodge.

The beaver that Hodgdon observed extensively at close range always began lodge building by at least starting to dig a burrow under water. When the bottom was too rocky for burrowing, these beaver went through the motions of digging before piling up material that eventually became a lodge. But Richard (1980, 95, fig. 53) describes a large lodge that had been constructed when a flood inundated the beaver's burrow and which was later exposed after falling water level left it high and dry. The lower portion was entirely composed of sticks piled up by the beaver, through which an access tunnel had been excavated. This led into a chamber above the highest water level large enough for two persons to squeeze into. Since the actual construction of this lodge was not observed, there is no way of knowing whether the beaver began with an attempt at burrowing.

Aeschbacher and Pilleri (1983, 98) found that when captive beaver built a lodge, they "cut sticks of two different lengths from the branches provided, peeled them and inserted the longer ones into the roof of the main chamber and the shorter ones into the chamber entrance, in a more or less radial pattern which was afterwards plastered with mud, wood shavings and small twigs." Richard also describes cases where the beaver gathered appropriate material before starting to build, suggesting anticipation of the construction.

Under natural conditions beaver add to and alter lodges and burrows, so that these shelters are in a constant state of enlargement and modification, somewhat like medieval cathedrals. Lodges and burrows are often abandoned, even when the beaver remain in the vicinity and build new shelters. Even after they are abandoned, beaver lodges are substantial piles of material, sometimes two or three meters high and

five to ten meters long, and their remains can be recognized years later even though grass, bushes, and even trees may have grown up on them. Abandoned lodges are sometimes reoccupied and reconstructed.

In many cases, except when there are very young kits in a family lodge, the beaver move about from one burrow or lodge to another in the same pond or stream, so that a shelter occupied one day may be empty the next. One pleasant day in mid-May I came upon a pair of adult beaver and at least one youngster in a sort of "bower" under a fallen tree partially screened by surrounding vines and small branches but clearly visible from my kayak as I paddled down a small stream in the New Jersey pine barrens. The nearest lodge was three or four hundred meters away, and the very gently sloping shoreline provided virtually no opportunity for burrowing. These beaver had presumably come out or stayed out after daybreak although they must have had some other shelter. This "bower" was later converted into a typical small lodge by adding sticks, leaves, grass, and mud to the walls.

Beaver vary their lodge and dam building in different situations, and they use many sorts of material according to what is available. Some beaver adapt their building behavior to atypical situations, such as ones that built lodges inside caves (Grater 1936; McAlpine 1977; Gore and Baker 1989). They may modify human artifacts—for example, adding sticks, mud, and even stones to a concrete dam and thus raising the water level above what the human dam builders intended. Or they may build nesting chambers inside abandoned, or even occupied buildings close to streams, such as unused mills (Richard 1980). These modifications of behavior suggest sensible use of available resources rather than the unfolding of rigid, stereotyped genetic programs.

One of the principal foods of beaver is the bark of trees, but they also eat other vegetation such as tubers of water lilies dug up from the bottom of their ponds. They may totally consume small branches up to about a centimeter in diameter; but from larger branches or the trunks of saplings they strip off only the bark and leave a shiny bare surface mottled by characteristic tooth marks. Their digestion is aided by symbiotic microorganisms, and their intestine, like that of most herbivorous mammals, has large branches or caecae where slow digestive processes take place. Beaver produce two kinds of feces, one of which they eat and thus recirculate some foodstuffs, presumably accomplishing in this way a more complete digestion of otherwise intractable materials.

Cutting trees is perhaps the best known of beaver activities. Most trees cut by beaver are no more than 15 to 20 cm in diameter, but occasionally a trunk as thick as one meter is severed. When the tree falls,



most or all of the branches are cut into smaller sections that the beaver can tow through the water. The bark may be eaten immediately, or sections of tree trunk and branches may be transported to underwater food piles near the lodge or burrow. Beaver tend not to use tree trunks or branches with edible bark for building lodges and dams. For these they usually employ sticks or logs from which the bark has been stripped, dead trees or fallen branches, and portions of trees whose bark is inedible or is eaten only rarely. When accumulating underwater food piles or building dams, beaver sometimes actively thrust one end of a stick into the mud or the previously accumulated tangle of branches; this prevents the stick from floating to the surface or being carried away downstream by the current.

Although these activities seem directed toward an end result that is useful to the beaver, they are by no means perfectly efficient. Some trees are cut halfway through and then abandoned, others lean against neighboring trees as they begin to fall, so that the beaver obtains no food at all. Beaver do not seem to realize in such cases that by felling the tree against which the first tree has lodged they could obtain a double supply of bark rather than nothing at all. Occasionally one finds tree trunks that have been cut partway through at two or more levels. Beaver of different sizes can chew effectively at different distances above the ground, or such multiple cuts may result from activity with and without an appreciable depth of snow. But they sometimes occur in areas such as the New Jersey pine barrens where there is not enough snow to account for them on this basis.

Inspection of areas where beaver have been working shows that they expend more effort than what we can see would be necessary. Even after branches or tree trunks are brought to ground level they may be cut into sections as short as 15 to 20 cm, although sticks as long as two or three meters can be transported; these short sections may be taken into the lodge where the bark is eaten, or the whole piece may be shredded to form bedding. It is easy for us to judge from inspection of beaver works that they could have accomplished their apparent objective with much less work than was actually expended. But lack of perfect efficiency in accomplishing an operation does not prove the lack of any conscious plan.

Beaver dams are built by gradually adding sticks, mud, and occasionally stones to some relatively narrow portion of a flowing stream. I have weighed stones up to 3.3 kg from a small dam, and Richard (1983) reports use of rocks as heavy as 10 kg. Ordinarily the dam is begun where there is already some small obstruction to the flow of water such

as a small stick or a rocky ledge on the bottom of the stream. As the water level rises more material is added, usually with most of it placed where the water is flowing most vigorously. Richard points out that laying sticks roughly parallel to the direction in which the water is flowing gradually produces, as the dam grows higher, an array of sticks oriented at increasing angles to horizontal. But many sticks are oriented in other directions, so that the eventual dam is a tangle of branches and mud. Manmade objects are sometimes also incorporated into beaver dams, such as pieces of sawed lumber or plastic. Although beaver apply mud and soggy vegetation to the upstream face of their dams, this does not produce a watertight structure, and usually more water trickles through or under a beaver dam than flows over the top. But beaver dams do commonly maintain a pond that may be a meter or more deep on the upstream side of the structure.

Wilsson (1971) and Richard (1967, 1980) have tested the hypothesis that the sound of running water is a stimulus to placing material on what will eventually become a dam. Playbacks of recorded sounds of running water did elicit piling of material close to the loudspeaker; but often this response occurred only after a considerable period of time. Richard (1967) found that playbacks of the sound of running water attracted the beaver's attention, but that lowered water level and inspection of the leaking dam led to the placement of most material where it was needed to stop the leak. When pipes were inserted through the dam, the beaver initially tried ineffective measures, such as placing mud on the dam itself near the noisy outflow from the pipe. In many cases, however, they eventually discovered the place where water was entering the pipe, and plugged this opening, even when it was several meters upstream from the dam and near the bottom of the pond. In one experiment a long pipe with a strainer at its entrance was arranged so that water entered the pipe well above the bottom of the pond and far upstream from the dam. The beaver eventually piled material under the strainer to create an underwater shoal, to which they then added enough mud and vegetation to plug the strainer and stop the escape of water.

Although sounds are clearly *one* stimulus to dam building, these experiments show that adding of material to a dam is by no means a rigid response to this particular stimulus. Most material is added on the upstream side of the dam even though the loudest sounds of running water are usually on the downstream face. Under natural conditions beaver pile material only at a few of many places where water is tumbling noisily. When beaver are adding small amounts of material to some of the

places where water is flowing out of the pond they are occupying, they often bring nothing at all to larger leaks where a much noisier flow is occurring. If the sound of running water were the only stimulus for dam building, one would expect to see piles of sticks and mud at many places where the sound of running water was present; but this is far from being the case. The view that dam building is a simple, fixed action pattern released uniquely by the sound of running water is a typical reductionistic oversimplification.

Beaver dams are often damaged by strong currents after heavy rains and snowmelts, and beaver usually repair breaks in actively maintained dams; but this may not happen for hours or days. Dam building and repairing is more prevalent in late summer and fall than earlier in the year. Occasionally, however, an especially disastrous break elicits strikingly energetic and appropriate behavior. One of the best examples of such emergency responses is described by Ryden (1989) in the course of extensive observations of a beaver colony whose members were cutting only a few trees because they were feeding primarily on water lilies. These beaver were relatively habituated to human observers whose presence did not seem to alter their normal behavior. For several weeks the adult male had been doing most of the dam maintenance. At nearly the same time every evening he inspected it and added small amounts of mud here and there; but his mate and the yearlings rarely visited the dam.

Then one day in late June, human vandals tore open a large hole in the dam, causing a torrent of water to rush out of the pond. The water level dropped at a rate that clearly threatened to drain the pond within a matter of hours. Ryden and a companion were naturally outraged at this wanton destruction and sought to reduce the damage by piling large stones in an arc upstream from the opening in the hope that this would slow the flow of water and help the beaver repair their dam, even though almost all of the stones were underwater. When the adult male emerged from the lodge at the normal time in the late afternoon and made his customary visit to the dam, he immediately responded to this emergency with drastically altered behavior. He first cut a few small branches and towed them to the gap in his dam where he succeeded in pinning some into the newly placed rock pile, although others washed away downstream.

At this pond there were very few dead trees available for the beaver to gather as dam building material, primarily because human picnickers had used them for firewood. In this emergency situation the beaver cut and brought to the dam green vegetation that he would otherwise have

used for food if he cut it at all. Three other beaver from the colony joined in relatively fruitless efforts to fix branches to the top of the rock pile over which the water was cascading, although during many nights of observation they had seldom been observed at the dam.

When adding branches to the top of the largely submerged rock pile failed to slow the torrent that was draining their pond, the beaver changed their tactics within a few minutes. Instead of towing more branches to the hole in the dam, they dove to the bottom of the pond, gathered mud and vegetation such as water lily stems, leaves and roots, and used them to plug the underwater gaps between the rocks. This slowed the escape of water from the pond, and in time the combined efforts of the beaver and their human helpers stabilized the water level, but at a much lower level than that of the original pond. Beaver ordinarily gather mud and underwater debris and apply such material to the upstream face of the dam *after* they have piled sticks at one of many places where water is flowing. But in this case they seemed to recognize that stick piling was ineffective and turned instead to plugging underwater gaps between the stones, even though the noise of flowing water came from the top of the rock pile.

Ryden watched the beaver work for most of the night at this dam-repairing endeavor, leaving only in the early hours of the following morning for a brief rest. When she returned, the beaver had retired to their lodge. Late in the afternoon, at his customary time of emergence from the lodge, the adult male's first act was to remove a large stick from the lodge itself and tow it 100 meters to the dam for further repair efforts. Ryden had been watching the beaver pond continuously for two hours beforehand, and in all probability this beaver had not visited his dam since retiring some twelve hours earlier. Yet he performed this most unusual action of removing a branch from the lodge and towing it to the dam, presumably because he remembered the need for material to repair the damaged dam. Other beaver also removed sticks from the lodge when they emerged and brought them to the dam.

While the beaver were inside the lodge, Ryden and her companion had brought many dead branches to the pond to provide the beaver with material for dam repair. They did this because there was so little available near the shores of this pond. On finding this floating tangle of branches, the beaver began at once to use them for dam repair, piling many of these branches on top of the material they had added to the arc of stones the night before. In time they succeeded in restoring a functional dam. Meanwhile the water had fallen so low that the entrances to the lodge sheltering a litter of kits had become exposed. Some days later

the beaver reconstructed the entranceways so that these were again underwater.

Further dam building with sticks and mud gradually raised the water level, but only slowly over many days. During this period, despite the lack of any very noisy flow of water, the beaver added material to the top of the dam, and above the water level. This is something they do not ordinarily do when building a dam, although Hodgdon (1978, 209) describes other instances of "over compensation of repair efforts . . . where repaired dam segments became higher than the normal dam crest"; and similar behavior is reported by Wilsson (1971) and Richard (1967). Ryden, however, has observed many repair efforts in which the top of the dam was kept almost perfectly level and is no higher at the point where a break had been repaired. In these situations when beaver adapt their behavior to changing circumstances, are they perhaps hopefully anticipating a higher water level that would restore their pond to its former depth? Of course one cannot be at all sure of such a speculative inference, but it is a possibility worthy of further investigation. One way to learn more about this behavior would be to inquire whether such "overcompensation" occurs only, or primarily, when the break being repaired had lowered the water level below its former level. Or is it just as likely to occur after a relatively small break that has not resulted in a significant drop in water level?

Ingold (1988, 97) claims that only members of our species ever plan things out "on those occasions when a novel situation demands a response that cannot be met from the existing stock-in-trade of habitual behaviour patterns." Such drastic breaks in a beaver dam as the one described by Ryden are fortunately rare events, and it is highly doubtful that these beaver had ever before encountered a problem of this magnitude. They certainly had never experienced human helpers placing large stones in an arc upstream from a major break in their dam. Their first response was to bring branches to the damaged dam and try to pin sticks into the stone pile. But they soon changed their behavior to digging up mud and vegetation from the bottom of the pond and using it to plug underwater spaces between the stones. Later they transferred material from lodge to dam. These were novel and appropriate responses to a wholly new situation without precedent in their experience.

Beaver often rework material they have built into their lodges, not only adding new branches and mud but shifting material to new positions. The taking of branches from the lodge sheltering young kits for

use in dam repair observed by Ryden is an extreme example. Even the dams are sometimes modified by removal of material as well as by addition of sticks, mud, or stones. In winter beaver ponds in northern latitudes are often frozen over for many weeks. During this time the beaver must either remain in the lodge or swim underwater beneath the ice, holding their breath, to reach their food storage piles or to travel to other parts of the pond. Several observers, including Wilsson (1971), Hodgdon (1978), and Ryden (1989), have noted that beaver sometimes open holes in their dams, thus causing the water level to drop and creating an airspace under the ice. Such holes in the dam have not been reported under other circumstances, to the best of my knowledge. Otters also make openings in beaver dams, as described by Reid, Herrero, and Code (1988), but their openings are usually trenches at the top of the dam rather than tunnels.

Opinions differ as to why beaver cut holes in the dams they have so laboriously constructed and maintained in previous weeks or months. One possibility is that the resulting air space under the ice makes it unnecessary to swim under water to reach their food stores or to travel farther from the lodge and perhaps reach openings in the ice through which they can come out on land to seek fresh food. Hodgdon (1978, 124–25 and 209–10) observed twenty-two beaver families during long periods in midwinter when they were confined under thick ice for weeks at a time. Eighteen of these family groups cut thirty-one holes in their dams, six being “beaver-sized tunnels completely through dams.” Most of these beaver-created breaks were made in the late winter when rising water levels probably began to flood the lodge. They lowered the water level by as much as half a meter, although usually they produced a 10 to 15 cm air space under the ice. The important point is that the beaver reversed their normal behavior with respect to their dams, cutting holes rather than adding material. It seems reasonable to suppose that they had some objective in mind, unless, like Ingold, we refuse to consider the possibility of any sort of conscious intention on the part of beaver.

To account for such reversal of their customary behavior of adding material to dam or lodge as the thoughtless unfolding of a genetically determined program requires that we postulate special subprograms to cover numerous special situations such as rising water in midwinter when the pond is covered by ice. Such postulation of a genetic subprogram can always be advanced as an explanation of any behavior that is observed; but the plausibility of such “ad hocery” fades as their number and intricacy increases. A simpler and more parsimonious explana-

tion may well be that the beaver thinks consciously in simple terms about its situation, and how its behavior may produce desired changes in its environment, such as deeper water when there is no pond, or an air space under the ice in midwinter under the conditions where Hodgdon observed that a large majority of beaver families cut holes in the dams they had previously constructed.

## *Tools and Special Devices*

**T**he use of tools by nonhuman animals has often been considered a sign of intelligence, and at one time it was believed to be limited to our closest relatives, the apes and monkeys. But prolonged and intensive observation of animal behavior has revealed many instances of tool use, and even of preparation or construction of simple tools, in a wide variety of animals ranging from insects to birds and mammals. Some scientists such as Hall (1963) have reacted against the trend to interpret tool use as especially telling evidence of rational behavior by arguing that it is not so special after all. Beck (1980, 1982) and Hansell (1984, 1987) have both reviewed the many known cases of tool use by animals, but they have also expressed the opinion that the use or even the preparation of tools does not necessarily indicate greater mental versatility than many other kinds of behavior.

Other types of animal behavior, such as the shell dropping by gulls described in chapter 2, are just as strongly indicative of thinking as tool using. But the latter is certainly *one* important category of behavior in which it would appear especially valuable for an animal to think consciously about what it is doing. Even in relatively simple cases of tool use, the object used as a tool is something different from whatever the animal uses it for. In an especially impressive type of tool preparation and use, a chimpanzee breaks off a suitable branch, strips it of twigs and leaves, carries this probe some distance to a termite nest, pokes it into termite burrows, and then pulls it out and eats with apparent relish the termites that cling to it. Such tool use differs significantly from digging up burrowing prey or otherwise capturing it by direct action, because all but the final steps require seeking out, modifying and manipulating something very different from the food that is thus obtained.

Although other types of behavior also entail acting on objects quite different from those involved in the final consummatory behavior, tool use, and especially the preparation of tools, constitutes an especially dis-



tinct separation of specialized behavior from the goal attained. To be sure, when a rat runs through a maze or a pigeon pecks a lighted key, these actions also differ from obtaining food from the end of the maze or from the magazine of a Skinner box. But selecting a suitable object to use as a tool entails a more independent action on the animal's part, the adaptation of an otherwise unimportant object such as a branch or twig to a specific purpose. Therefore it is appropriate to retain much of the commonsense view that tool use, and especially tool manufacture or preparation, are rather special, although of course not uniquely indicative of conscious thinking on the animal's part. This chapter will review not only significant cases of tool use in the customary meaning of that term, but two other cases of specialized behavior by birds that are akin to tool use in strongly suggesting simple thinking about something the animal is trying to accomplish.

Although tool use is relatively rare, it does occur consistently in many groups of relatively complex animals. The suggestive examples mentioned below, as well as many others, are clearly reviewed by Beck (1980). Certain crabs pick up anemones (which give off stinging nematocysts when disturbed) and either hold them in their claws to ward off attackers (Duerden 1905; Thorpe 1963) or hold them close to parts of their exoskeletons so that the anemones attach themselves and form a protective outer covering (Ross 1971). Ant lions and worm lions were mentioned in chapter 4 because the pits they construct are functional artifacts. But their prey-catching behavior also includes the throwing of small grains of sand at the ants or other small insects that fall into their pits, and this constitutes a simple form of tool use, as described by Wheeler (1930) and Lucas (1989). But the ant lion does nothing to modify or improve the grains of sand or other small particles that it throws. It is not even clear that the throwing is particularly directed at the prey.

Other insects, however, carry out more specialized tool-using behavior. Ants of the genus *Aphaenogaster* use crude sponges to carry back to their nests semiliquid foods such as fruit pulp or the body fluids of prey, as described by Fellers and Fellers (1976). They pick up bits of leaf, wood, or even mud and hold them in the liquid long enough for appreciable amounts to be absorbed before carrying back the wetted, sponge-like object to the colony. This enables them to transport as much as ten times as much of the liquid food as they could otherwise carry. Wasps of the genus *Ammophila* and *Sphex* hold in the jaws a small pebble, a piece of wood, or other small object and use it to tamp down soil used to

close a burrow where they have laid an egg, as reviewed by Evans and West Eberhard (1967) and Beck (1980). An example of this type of behavior has recently been described in detail by Haeseler (1985). Finally, the use of silk secreting larvae by the weaver ants, described in chapter 4, involves the use of these living tools during the construction of the leaf nests.

An especially striking case of complex tool use is presented by McMahan's discovery that certain neotropical assassin bugs "fish" for termites with the corpses of previous victims. These insects actually employ two different types of tool when capturing termites. First they pick up articles from the outer surface of the termite nest and apply them liberally to the outer surface of their own bodies. This apparently provides as an effective sort of camouflage, whether tactile, olfactory, or both. Then, having caught one termite at an opening into the nest and sucking its internal juices, the assassin bug dangles the corpse into the opening, where it attracts other termites that are captured in turn. One assassin bug was observed to consume thirty-one termite workers by means of this combination of camouflage and baiting (MacMahan 1982, 1983).

Many cases of tool use by birds have been reviewed by Chisholm (1954, 1971, and 1972). Usually these involve using some small object such as a twig or piece of bark to remove an edible insect from a crevice where the bird cannot otherwise reach it. The bird may simply pick up a suitable probe or it may break off a twig and bring it to the crevice from which it evidently wants to remove an item of food. Sometimes birds such as the marabou storks observed by Marshall (1982) seem to be trying unsuccessfully to probe for food with sticks. One of the best-known examples of such tool-assisted food gathering is practiced by two species of Darwin's finches, discussed in chapter 2 with reference to the specialized habit of feeding on the blood of boobies. *Cactospiza pallida* pries insect larvae, pupae, and termites from cavities in dead branches with the aid of cactus spines or twigs held in its beak, and *C. heliobates* uses similar tools to remove prey from crevices in mangroves (Curio 1976, 164-65; Grant 1986, 3, 372).

Bowman (1961) and Millikan and Bowman (1967) studied the learning of such tool-using behavior by captive Galapagos finches, and Jones and Kamil (1973) observed that a captive bluejay learned to use probes and pieces of paper to obtain otherwise inaccessible food. Somewhat similar tool use by green jays in Texas has also been reported by Gayou (1982). Some of the hungry bluejays tore pieces of paper of

roughly appropriate size and shape from the sheets of newspaper lining the bottom of their cages and used the pieces as crude tools to rake into the cage food pellets that they could not otherwise reach. The behavior varied considerably among individuals; some did not learn it even when given abundant opportunity to observe other birds obtaining food in this way. It is thus anything but a stereotyped fixed-action pattern. It is possible that after failing to reach a food item with its bill a bird intentionally picks up and uses a twig or other object to aid in this endeavor. But many random movements seem to precede even the crude and occasional use of tool-like objects by captive jays.

Crows and their relatives are versatile and ingenious birds that sometimes use tools to a limited degree, as reviewed by Angell (1978). Reid (1982) reported that a young captive rook used a standard drain plug to close the drain hole in a depression in its aviary cage and thus to retain rainwater that would otherwise have escaped. Janes (1976) describes how a pair of nesting ravens dislodged small stones that fell in the general direction of two people who had climbed close to their nest and young. But Heinrich (1988, 1989) observed similar behavior by wild and captive ravens and believes that it may be "displacement behavior when they are angry or frustrated." When ravens are disturbed near their nest and young, they often strike at all sorts of available objects, so that twigs fall from branches on which they are perched; but, as Heinrich points out, the dropped objects have never been observed to strike the intruder.

Another type of tool use that has been observed in a few species of birds is throwing stones or other hard objects at eggs that are too strong to be broken by pecking or other direct attack. The best-known example is the dropping of stones on ostrich eggs by Egyptian vultures, as described fully by Goodall and van Lawick (1966). Just how this behavior is acquired is not clear, although Thouless, Fabshawe, and Bertram (1989) suggest that vultures first learn to associate small eggs that they can break with the food they obtain in this way, and then, recognizing large ostrich eggs as potential food, learn that these can be broken by having stones dropped on them. However this sort of tool use develops, it seems likely that the vultures are thinking about the edible contents of the ostrich egg as they pick up stones and drop them.

Heinrich (in preparation) has recently studied a specialized form of tool use by ravens that suggests insight into novel and somewhat complex relationships. Five ravens were captured as nestlings and held in large outdoor cages until they were well grown. The cage was equipped

with two horizontal poles well above the ground. The ravens had been fed for many months with road-killed animals and other pieces of meat placed on the ground within the cage. During the experiments Heinrich provided the hungry ravens with only a small piece of meat suspended from one of the horizontal poles by a piece of string. At first the ravens flew to the suspended food but were unable to detach anything edible from it; they also seized the string while perched on the horizontal pole, and pulled at it from time to time. But the string was too long to allow a single pull to lift the meat within reach. After six hours one raven suddenly carried out a complex series of actions that did bring the suspended meat within reach. This entailed reaching down, grasping the string in the bill, pulling it up, holding the string with one foot, releasing it from the bill, reaching down again to grasp the string below the pole, and repeating the sequence four or five times.

For a few days only this raven obtained suspended meat in this way, but in time all but one of its companions began to pull up the string, hold it with one foot and repeat these actions until the food could be reached directly. They performed this feat in slightly different ways; two birds moved sideways during successive stages of holding the string with the foot so that the string was held at different points along the horizontal perch. The other two piled the string in loops, standing in roughly the same spot while holding the string. All but the first raven to perform this string-pulling action could have learned it by observing the successful bird, but Heinrich's impression was that each bird solved the problem for itself, using slightly different maneuvers, although its efforts to do so may well have been encouraged by watching its companion obtain food in this unusual manner.

Heinrich also observed a further indication of real understanding by the ravens that had learned this specialized form of food gathering. When a raven is startled while holding a small piece of meat in its bill, it typically flies off without dropping the food. But all four of Heinrich's ravens that had obtained their food by the string-pulling maneuver always (in more than one hundred trials) dropped the meat before flying to another part of the cage. They apparently realized that the string would prevent the meat from being carried away. One raven never did learn to obtain food by string pulling, although it had obtained food from its string-pulling companions. When this less talented bird was startled while holding a piece of meat still attached to a string, it did fly off without releasing the meat—which was jerked from its bill when the string became taut. Two crows failed to obtain suspended meat by pull-

ing up and holding string; and they initially flew off with meat attached to a string, although they learned not to do so after five and nine trials respectively.

Small caged birds have been trained to obtain food by pulling on strings, as studied in detail by Vince (1961). But in all cases a considerable time of trial-and-error behavior was necessary before the trick was learned. In Heinrich's experiment the four successful ravens seem to have had the insight that pulling and then holding the string would bring the food within reach. Each bird carried out the whole sequence the first time it was attempted, holding it with the foot, and repeating the process at least four times. Heinrich had watched the ravens at all times when food was suspended from a string in their cage, and they did not engage in partial or incomplete actions that gradually developed into a successful food-gathering procedure. They had never had access to strings or stringlike objects such as vines; and in his extensive observations of wild and captive ravens Heinrich has never seen them pulling on vines or other stringlike objects to obtain food.

Tool use by mammals is not widespread; except among primates and elephants it is scarcely more prevalent than with birds. Beck (1980) describes simple cases of tool use by three species of rodents, tool-assisted digging by a pocket gopher that held small stones or other hard objects between the forepaws, the leaning of an oat stalk against the wall of a glass aquarium by a captive harvest mouse that used it to climb to the top of the enclosure, and the throwing of sand at snakes by ground squirrels. Rasa (1973) has described how the dwarf mongoose breaks eggs by throwing them backwards between its hind legs against some hard object. Elephants are trained to hold various objects with the trunk, and wild elephants have been observed to use sticks to scratch at parts of the body that are difficult or impossible to reach directly. They also throw things held with the trunk, although this is apparently not a common occurrence.

The clearest case of tool use by mammals other than primates and elephants is the use of stones by sea otters, as described by Kenyon (1969), Calkins (1978), Houk and Geibel (1974), Riedman and Estes (1990) and Riedman (1990). Stones are carried to clams, abalones, or other molluscs at the bottom and used to hammer them loose from the substrate. Stones are also carried to the surface and used as anvils resting on the otter's chest as it floats on its back and hammers shellfish or sea urchins against the hard surface. Riedman has observed much individual variability in the ways in which sea otters use stones or other objects such as shells as anvils against which to hammer recalcitrant shellfish.

They sometimes keep a favorite stone tucked under the armpit for repeated use. Some otters use discarded bottles as anvils instead of stones (Woolfenden 1985). Others have learned that small octopi retreat into empty aluminum cans; these otters have been observed to bring the occupied can to the surface, where they tear it open with the teeth to extract and eat the octopus (McCleneghan and Ames 1976). It would seem helpful to think in simple terms about the food they hope to obtain by these specialized procedures.

Some species of primates engage in tool use quite often, but others do so rarely if at all, as reviewed in detail by Beck (1980). Most of the objects used as tools are stones or pieces of wood, which are used to break open nuts or to throw at other animals or people. Parker and Gibson (1990), Westergaard and Fragaszy (1987), and Chevalier-Skolnikoff (1989) have provided extensive reviews of tool use and manufacture of simple tools by monkeys and apes. Chimpanzees and Capuchin monkeys (genus *Cebus*) are clearly more inclined to make and use tools than other species. Some but not all captive capuchin monkeys display considerable inventiveness in fashioning probes used to obtain otherwise inaccessible food and sponge-like tools to take up liquids. Ritchie and Fragaszy (1988) describes how a mother Capuchin "manufactured, modified, and used simple tools to manipulate her infant's head wound, and applied modified plant materials to the wound." Westergaard and Fragaszy conclude that they are almost as versatile in this type of behavior as chimpanzees. Chevalier-Skolnikoff (1989) concludes from her review of tool use by capuchins that in some individuals this behavior conforms to all six of Piaget's stages of sensorimotor intelligence. The many commentators on her review express a wide range of mutually contradictory interpretations, but it seems clear, on balance, that regardless of theoretical debates, these monkeys, as well as the Great Apes, must think about the objectives they are achieving by the use of tools.

It is important to emphasize that although some individual monkeys and apes become very proficient makers and users of tools, others never do anything of the kind, even under virtually the same environmental conditions. Furthermore, the details of tool making and using vary widely among individuals, and across populations of the same species. For example, the well-known manufacture and use of sticks to "fish" for termites varies in detail among populations of chimpanzees in different regions of Africa, as reviewed by Sugiyama and Koman (1979), McGrew, Tutin, and Baldwin (1979), and Goodall (1986). Captive apes have been trained to use a wide variety of human devices from

socket wrenches to bicycles. An orangutan has even been taught to make stone tools (Wright 1972), although of course this is not something that they do under natural conditions.

As described in chapter 1, Boesch and Boesch-Ackermann (1984, 1991) have observed that chimpanzees use different kinds of stones for cracking different sorts of nuts, and remember where both stones and nuts are to be found, so that when a particularly tough species of nut is gathered they know where to find an appropriate type and size of stone with which to open it. They use stones in a variety of well-coordinated ways to open different types of nuts. Indeed their manual dexterity in this activity has led to likening them to early hominids.

Like all the instances of versatile behavior discussed in this book, one can postulate that whatever tool making and tool use may be displayed by animals, it need not necessarily be accompanied by, much less be influenced by, any conscious mental activity. But, as pointed out in chapter 1, this is a very difficult question to answer with any confidence, and therefore *negative* assertions are just as questionable as positive ones. One can invert the customary reason for doubting the presence or influence of conscious thinking when animals behave in a versatile and ingenious fashion by asking how one can prove that they are *not* conscious of what they do.

### Burying and Cooling Young

Egyptian plovers (*Pluvianus aegypticus*) resemble the migratory plovers of North America, but nest on sandbars on the shores of African rivers. Herodotus, who called this bird the Trochilos, and others more recently, have stated that it picks leech-like parasites from the teeth of crocodiles. It is no longer found in Egypt because of climatic and ecological changes since ancient times. In 1977 Thomas Howell (1979) studied Egyptian plovers that were nesting along the Baro River in southwest Ethiopia. While he and other recent observers have not seen them picking the teeth of crocodiles, the behavior patterns they use to conceal their eggs and young and to protect them from overheating are in many ways more striking and significant.

Egyptian plovers nest only on sandbars exposed during the dry season. When nesting they are very aggressive towards predators on eggs or young and towards other Egyptian plovers as well as other birds that eat the same types of food. Their nest is a simple depression in the sand, known as a scrape. Only island sandbars are selected for nesting, and very similar sandy areas connected to the mainland are avoided. This

probably reduces predation on eggs and young by mongooses, which apparently do not venture into even shallow water, as some nests were on islands separated from the shore by only about a meter with the intervening water depth only about 10 cm. Both male and female Egyptian plovers make several scrapes before eggs are laid in one of them. As Howell (1979, 24–37) describes this behavior “A pair may make dozens of scrapes before finally settling on a nest site, and a small islet may resemble a miniature battlefield pocked with bomb craters.”

As soon as an egg is laid it is covered with sand by use of the bird's bill. Both parents take turns sitting on the nest during most of the daylight hours; while incubating eggs they sometimes remove the sand and bring the egg in contact with the incubation patch (an area on the ventral surface where the feathers are much thinner than elsewhere so that the egg can come in contact with the skin). Incubation is almost continuous during the night, and the eggs are about two thirds covered with sand. During the six hottest hours of the day, when the temperature in the shade rises to 45 degrees Centigrade and over 50 degrees in the sun, each adult frequently soaks its ventral feathers in the river and returns to settle on the buried eggs, thus surrounding them by wet sand which keeps the eggs distinctly cooler than they would otherwise be.

The action of wetting feathers is distinctly different from wading in the river in search of food, which involves wetting only the feet and lower legs. Quoting Howell again, “to soak, an adult Egyptian plover wades into quiet, shallow water at the river's edge until its ventral body surface is immersed. The bird then rapidly rocks up and down, alternately lowering and raising its fore- and hindparts in an antero-posterior plane. . . . On reaching its nest, the bird fully extends the wet ventral feathers and settles on the substrate, often with widely spread legs. . . . As the ambient temperature rises and nest-soaking behavior commences, the parents quickly shorten the intervals between changeovers (from one to several hours when it is cooler) and may relieve each other every few minutes.”

The chicks are precocial and do not return to the nest after their first day. The parent birds bring food to them and expose food for them by turning stones. Howell describes the response to approaching predators: “The chicks crouch down and are completely covered with sand by a parent in the same manner that eggs are covered. Buried chicks are also wetted with soaked ventral feathers. . . . Even juveniles up to three weeks of age may be covered with sand by a parent.” If an approaching kite or pied crow is spotted at a considerable distance, the parents manage to cover the chick so thoroughly that Howell found it nearly impos-



sible to locate it. When human or other predators approach a nest on very hot days the parents continue the soaking behavior even though they act nervously when doing so. This of course risks disclosing the nest location, but apparently the danger of overheating is so great that this behavior is worth the risk.

Other species of waders related to the plovers are known to soak belly feathers and wet their eggs or young when the temperature is very high (MacLean 1975). But this habit reaches an extreme form in the sandgrouse that nest in the Kalahari desert of southern Africa (Cade and MacLean 1967; MacLean 1968). These birds nest far from the few rivers where water is available, and they concentrate there in large flocks even when raising young at nests that are far away—in extreme cases as far as 80 kilometers. The males, but not the females, have specialized feathers on the ventral surface that can hold up to 25 to 40 ml of water. Even after flying for miles these feathers still retain 10 to 18 ml. When it is very hot, the chicks go to males, which squat over them and wet them with the water-carrying feathers.

Egyptian plovers wet their eggs or young only when the temperature rises above roughly 40 degrees. They need only go a short distance to the river to gather water for this purpose; but the male sandgrouse must add to its own drinking behavior the special action of wetting its ventral feathers and then flying many miles to where its chicks are located. The end result of the specialized behavior is far removed in space and time from the situation in which the belly feathers are wetted. Although we cannot accept this displacement as conclusive evidence that these birds think about keeping their eggs and young cool when they wet their feathers, the whole pattern is at least suggestive.

### Fishing Techniques of Herons

Herons are specialized for catching fish and other prey by a very rapid stabbing motion of their long thin bills. This action consists of an extension of their elongated necks, which have been curved back into a compact resting position beforehand. Prey are ordinarily seized in the slightly opened bill, although the motion is so fast that the heron seems to be stabbing, and on rare occasions it may actually impale a fish. Herons have excellent vision and aim quite accurately at fish, crayfish, or other prey even when they are underwater. They usually forage in quite shallow water, so that refraction of light at the surface is probably not a serious problem. The impression one gathers from reading general ac-

counts of heron behavior is that they obtain their food by standing still and watching intently until they see a fish or other prey and then strike at it so fast that the human eye cannot follow details of the motion. But the prey is seldom so obliging as to make itself readily available, and herons often spend long periods waiting or searching before they strike, and sometimes succeed in seizing an edible morsel. In an apparent effort to improve their chances of success, some herons display a degree of versatility in their feeding techniques that suggests that they are thinking about what they are doing.

Several specialized fishing techniques of North American herons have been described by Meyerriecks (1960), and recent observations by Higuchi and others demonstrate that one species occasionally uses bait to attract fishes. Because they have been observed to use a variety of feeding techniques, I will consider here primarily the green-backed heron (now known as *Ardeola striata* although other scientific names have been applied to it in the past) and the reddish egret, *Dichromanassa rufescens*. But most of these special techniques are also used by other species on some occasions. The simplest procedure adopted by hungry herons is to stand and wait with the neck retracted and to stab at small fishes or other prey when they appear within striking distance. While herons typically feed in shallow water, they also sometimes hunt for insects on land or snatch flying insects from the air. Often no prey is sighted during long periods of standing and waiting, and the heron begins to walk slowly, usually wading in shallow water. As Meyerriecks (1960, 8) describes this behavior of green-backed herons: "As the bird stalks closer to its prey, its steps become slower and longer; each foot is brought forward, placed, and then lifted so slowly that the movements are barely perceptible. . . . The bird may retract its head and neck or hold them extended over the water or ground; or rarely the head and neck are held momentarily in an extended 'peering over' attitude."

Herons sometimes add "wing flicking" to their slow and careful walking in search of prey. As Meyerriecks describes this in the great blue heron, *Ardea herodias*, the bird "suddenly extends and withdraws its wings about a foot in a short, rapid flick. Such wing-flicks may be repeated as many as five or more times, but usually two or three flicks in rapid succession are made, and then the bird resumes wading. I have seen wing-flicking only on bright days, in open, shallow water, when each wing-flick created an obvious sudden shadow on the surface of the water. The function of wing-flicking is to startle prey" (Meyerriecks 1960, 89). The reddish egret spends less of its feeding time standing

and waiting or walking slowly, and wing-flicking is quite common. Again quoting Meyerriecks (1960, 108), its most common feeding technique

is a lurching, weaving type of half-run, half-jump progression. As the bird reels forward, it stabs rapidly to the right and left, attempting to seize any prey disturbed by its activities. This method is used primarily in very *shallow* water. . . . Open Wing Feeding is another characteristic feeding technique of *rufescens*. The feeding bird begins by running slowly, wings partly extended. Then at the sight of the prey it runs rapidly and extends the wings fully. As the prey dash about, the egret turns and twists, wings still extended fully, and the bizarre performance may continue for several minutes. On occasion the bird may halt suddenly in the middle of a run, retract one wing, rapidly extend and retract the other wing, and then resume its forward run.

Reddish egrets frequently change from the sort of open wing feeding described above to what is called canopy feeding. As Meyerriecks (1960, 108–109) describes canopy feeding by the reddish egret, the bird

runs forward with the wings extended, then halts and peers into the water, and then brings both wings forward over its head, forming a canopy over the head and neck. This pose is held for a few moments to several minutes. I could clearly see the rapid fish-catching movements the bird made under the canopy of the wings. . . . My observations of *rufescens* at extremely close range (three feet) indicate that the shadow provides a false refuge for the fish startled into motion by the previous dashing activities. Reddish egrets typically hold their wings in the canopy attitude for a minute or two *before* they make a strike. I could clearly see many fish enter the shade of the canopy in the shallow water, and when a number of prey had thus “fallen for the ruse,” the egret would stab rapidly under its extended wings.

This is also a common behavior pattern of the African black heron, *Melanophox ardesiaca* which employs canopy feeding extensively, and Winkler (1982) found that they attracted more small fishes when canopy feeding than would otherwise have come within their reach.

Another food-gathering procedure observed by Meyerriecks (1960, 109) in the reddish egrets is foot-stirring:

As the egret waded forward rather slowly, it would vibrate its feet over the surface of the mud, imparting a scraping motion to the feet; then it would stop and peer at the surface of the water and either strike at prey or move on, usually resuming the scraping motions. Hovering-stirring is an aerial variant of typical stirring or scraping. The feeding bird moves forward slowly, then suddenly launches into flight, hovers over the surface of the water, and very gracefully

scrapes the mud or aquatic vegetation with one foot. This behavior is repeated while the bird continues in flight. The strike is made from the hovering position.

Foot-stirring is also used by snowy egrets, *Leucophoyx thula* and other herons (Meyerriecks 1959; Rand 1956). Another variation on this theme is vibrating the bill while it is in contact with the water. Kushlan (1973) has found that this also attracts small fish which the heron then captures.

All of these specialized types of feeding behavior suggest that the heron is actively trying to detect or attract small fishes or other prey. Nothing is known about the development of these feeding techniques in the individual birds, or the degree to which they involve learning or genetic influences. A behavioristic interpretation would be restricted to noting that the obtaining of food would have reinforced immediately preceding actions, and an evolutionary view would emphasize the obvious adaptive value of obtaining food by these techniques. But the versatility of the behavior also suggests that the heron thinks consciously about these uses of its wings and feet to attract or startle prey and thus make them visible and catchable.

As discussed in chapter 1, the extreme example of specialized, and perhaps purposeful, feeding techniques of herons is occasionally exhibited by the green-backed herons, *Ardeola striata*. While most of these birds feed in relatively simple ways, they have occasionally been observed to use bait to attract small fishes (Lovell 1958; Sisson 1974; Norris 1975; and Walsh et al. 1985). Higuchi (1986, 1987, 1988a, 1988b) has studied this behavior intensively, both in Japan and in Florida. The herons pick up some small object, which may or may not be edible, carry it to an appropriate spot on the shore, drop it into the water and watch it intently. When small fish approach the bait the heron seizes them with its usual rapid neck extension. A wide variety of small objects are used as bait, including twigs, leaves, berries, feathers, insects, earthworms, pieces of bread or crackers dropped by human visitors to the park, and even bits of plastic foam. If the bait drifts away, the heron may pick it up and drop it again within reach.

Adult birds are more successful than juveniles, which suggests that learning plays a role in the acquisition of bait fishing behavior. Small fishes often come to the surface to nibble at such floating objects, and the heron seizes one with its characteristic stabbing motion. In some situations the heron may wait on a branch somewhat above the water level after throwing the bait out from the shore and then fly out to seize

fish attracted to the floating object. In Higuchi's initial observations only a few out of a colony of twenty or thirty green-backed herons nesting near a city park engaged in this type of fishing. He suspected that they had first observed small fishes attracted to pieces of bread dropped into the water by children, but he was unable to induce bait fishing by dropping crumbs near other birds of the same species. Further investigation will be necessary to learn just how a few individual herons acquire this specialized and enterprising behavior.

When no suitable small objects are available near the shore herons sometimes gather small bits of vegetation and bring them to the water's edge. They may even break twigs into smaller lengths for this purpose. It is important to recognize that only a very small fraction of the green-backed herons have been seen to use bait for fishing, but a bird that has acquired the habit does engage in bait fishing repeatedly. As with virtually all cases of enterprising behavior by animals, a behavioristic interpretation is quite possible. But it does seem more parsimonious to infer that the bird thinks about its behavior and the probable results.

*Concepts*

**T**he previous chapters have reviewed suggestive evidence that on some occasions animals may be consciously aware of objects and events, and that they experience perceptual consciousness, roughly corresponding to what Natsoulas calls Consciousness 3. But do they grasp any sort of generalizations, or is each perception experienced in total isolation from all others? For example, do animals ever think in terms of categories such as food, predators, or members of their own group? This is a difficult question to answer, like most of those discussed in this book, but it is an important one. The ability to classify and think about categories as well as specific individual items is a powerful facet of conscious thinking, and if it lies within the capabilities of various animals, this ability is an important attribute that must be appreciated to understand the animals adequately. Some evidence points in the direction of a capacity to think in terms of simple concepts, and this chapter reviews a few especially clear examples.

The natural world often presents animals with complex challenges best met by behavior that can be rapidly adapted to changing circumstances. Environmental conditions vary so much that for an animal's brain to have programmed specifications for optimal behavior in all situations would require an impossibly lengthy instruction book. Whether such instructions stem from the animal's DNA or from learning and environmental influences within its own lifetime, providing for all likely contingencies would require a wasteful volume of specific directions. Concepts and generalizations, on the other hand, are compact and efficient. An instructive analogy is provided by the fact that the official rules for a familiar game such as baseball run to a few hundred pages, although once the general principles of the game are understood, quite simple thinking suffices to tell even a small child what each player should do in almost all game situations.

It is of course obvious that we can classify stimuli into groups to

which an animal gives the same or a very similar response. But such evidence does not suffice to indicate that the animal thinks in terms of a category that includes all these stimuli. For example, hungry animals approach and eat a wide variety of foods and flee from a variety of dangers, but they might think about each one quite independently of all others and never think about the categories of edible or dangerous things. In social groups, individual animals often recognize other members of their group, or at least react differently to kin and nonkin (Fletcher and Michener 1987; Hepper 1990). For instance, honeybees are more likely to deliver food to their full sisters than to the half sisters that result from the queen having mated with more than one drone (Oldroyd, Rinderer, and Buco 1991). In an especially telling case, Porter (1979) observed that in a captive colony of the neotropical fruit bat *Carollia perspicillata*, when the harem male heard distress calls from a baby that had fallen to the floor, he would frequently crawl to the mother of that particular baby and stimulate her to retrieve her infant.

But do any animals think in terms of such categories as “one of us”? Differential reaction to group members or close relatives as compared with others of the same species might be based on familiarity versus strangeness and not entail any conscious thinking about the categories of group member or kin. Some of the best evidence that animals can think in terms of categories or concepts has become available from what at first thought may seem an unlikely source, namely the detailed analyses of animal learning by experimental psychologists that have been reviewed by Mackintosh (1974), Hilgard and Bower (1975), Dickinson (1980), and Bolles and Beecher (1988). To explain how these experiments came to be developed, it will be necessary to digress into a rather lengthy consideration of what life is like for the experimental animals used to study learning.

### Behavioristic Inhibitions

The investigation of the possibility that animals might think in terms of concepts or even categories of important objects has been seriously impeded because comparative psychologists have seemed to be almost petrified by the notion of animal consciousness, as reviewed by Burghardt (1985b). Historically, the science of psychology has been reacting for fifty years or more against earlier attempts to understand the workings of the human mind by introspective self-examination—trying to learn how we think by thinking about our thoughts. This effort led to conflicting and contradictory results; so, in frustration, experimental

psychologists largely abandoned the effort to understand human consciousness, replacing introspection with objective experiments. While experiments have been very helpful in analyzing learning and other human abilities, the rejection of any concern with consciousness and subjective feelings has gone so far that many psychologists virtually deny their existence or at least their accessibility to scientific analysis.

In one rather extreme form of this denial, Harnad (1982) has argued that only after the functioning of our brains has determined what we will do does an illusion of conscious awareness arise, along with the mistaken belief that we have made a choice or had control over our behavior. The psychologists who thus belittle and ignore human consciousness can scarcely be expected to tell us much about subjective thoughts and feelings of animals, still less the degree to which they think in terms of concepts. If we cannot gather any verifiable data about our own thoughts and feelings, the argument has run, how can we hope to learn anything about those of other species?

A long overdue corrective reaction to this extreme antimentalism is well under way. To a wide range of scholars, and indeed to virtually the whole world outside of narrow scientific circles, it has always been self-evident that human thoughts and feelings are real and important (see, for example, MacKenzie 1977; and Whiteley 1973). This is not to underestimate the difficulties that arise when one attempts to gather objective evidence about other people's feelings and thoughts, even those one knows best. But it really is absurd to deny the existence and importance of mental experiences just because they are difficult to study, and because it is very difficult to distinguish conscious from unconscious cognition in animals.

Why have so many psychologists appeared to ignore a central area of their subject matter when most other branches of science refrain from such self-inflicted paralysis? The usual contemporary answer is that the cognitive revolution discussed in chapter 1 has led to a newly dominant school of cognitive psychology, based in large part on the analysis of human and animal behavior in terms of information processing (reviewed by Baars (1986, 1988), Blakemore and Greenfield (1987), and Johnson-Laird (1988) among others). Analogies to computer programs play a large part in this approach, and many cognitive psychologists draw their inspiration from the success of computer systems, feeling that certain types of programs can serve as instructive models of human thinking. Terms that used to be reserved for conscious human beings are now commonly used to describe the impressive accomplishments of computers. Despite the optimism of computer enthusiasts,



however, it is highly unlikely that any computer system can spontaneously generate subjective mental experiences (Boden 1977; Dreyfus 1979; Baker 1981; Searle 1990; Churchland and Churchland 1990).

Conspicuously absent from most of contemporary cognitive psychology is any serious attention to conscious thoughts and subjective feelings. For example, Wasserman (1983) defended cognitive psychology to his fellow behaviorists by arguing that it is not subjective or mentalistic; but, as described below, some of his own experiments have come to indicate that animals can think in simple conceptual terms. Analyzing people as though they were computers may be useful as an initial, limited approach, just as physiologists began their analysis of hearts by drawing analogies to mechanical pumps. But it is important to recognize the limitations inherent in this approach; it suffers from the danger of leading us into what Savory (1959, 54) called by the apt but unfortunately tongue-twisting name of "the synecdochic fallacy." This means the confusion of the part of something with the whole, or, as Savory put it, "the error of nothing but." Information processing is doubtless a necessary condition for mental experience, but is it sufficient? Human minds do more than process information; they think and feel. We also experience beliefs, desires, fears, expectations, and many other subjective mental states.

Psychologists have analyzed learning in animals by means of a host of ingenious experiments, and whole books such as those by Dickinson (1980), Mackintosh (1974), and Roitblat (1987) are required to review them adequately. But these discussions of what animals learn and remember are couched almost entirely in behavioristic terms. The psychologists who have conducted and reviewed these sorts of experiments concentrate almost exclusively on what animals do, and avoided like a plague any consideration of what they might think or feel as they carry out the sometimes complex patterns of behavior they have learned will get them food or allow them to avoid unpleasant experiences. One notable exception was Tolman (1932) who emphasized that animals often appear to expect certain outcomes when they perform various learned behavior patterns, such as running mazes. Tolman called his viewpoint purposive behaviorism, and he clearly believed that rats and other animals intentionally try to obtain desired things such as food and to avoid unpleasant experiences like receiving electric shocks. But the positivistic *Zeitgeist* of his times was so influential that he refrained from explicit suggestions that animals might consciously think about what they were doing. Only toward the end of his long and distin-

guished career did he confess to having been a “cryptophenomenologist” (Tolman 1959).

Tolman’s ideas were not widely accepted by behavioristic psychologists, although in recent years he is often acknowledged as having anticipated the development of cognitive psychology in the 1950s and 1960s, as reviewed by Burghardt (1985). A few other psychologists such as Mowrer (1960a, 1960b), Bolles (1972, 1979), and Walker (1983) have rather cautiously ventured to suggest that processes more or less equivalent to conscious thinking must occur in certain animals. But they have almost always avoided explicit consideration of animal consciousness. Yet the learned behavior patterns studied by comparative psychologists can be appropriately viewed as versatile behavior by which the animal adapts to a novel and challenging situation, and does what it has learned will get it food or enable it to avoid something unpleasant. Rather than tediously pointing out that the experimental animal may have understood perfectly well that it had to do certain things to get food or avoid electric shocks, I will concentrate on some recent experiments that are even more strongly suggestive of simple conscious thinking. These are usually referred to in terms of concepts that the animals appear to have acquired.

### Experimental Analysis of Animal Cognition

The criticism that behavioristic psychologists have neglected animal thoughts has begun to elicit a promising new response. Several psychologists concerned with animal learning and problem solving under controlled laboratory conditions now claim that they and their colleagues have been investigating animal minds all along, even when behaviorism was dominant (Mason 1976; Roitblat, Bever, and Terrace 1983; Walker 1983). But in the same breath they are likely to assure us that all animal thinking, and even most human thinking, is quite unconscious. Mind is redefined as information processing; an analysis of how information is acquired, stored, and retrieved, and how it affects behavior, is felt to be all that is required to understand animal minds. But beyond this defensive reaction to the charge that a central aspect of psychology has been neglected, there is a positive and hopeful aspect to these discussions. This is the increasing recognition that when animals learn to perform new tasks, they presumably think, consciously or unconsciously, about the problems they face and the solutions they attempt or achieve. As experimental psychologists become increasingly concerned with mental

experiences in animals, their ingenious experimental methods can be adapted to the study of animal consciousness, once the taboo against its consideration is laid aside.

This process has been under way for some time, but it has remained hidden behind a smokescreen of behavioristic terminology. Many of the experimenters really do seem quite interested in the possibility of thinking, even of conscious thinking, in the animals they study. But they have been inhibited from saying so directly, even to themselves; and the result has been what I call semantic behaviorism (Griffin 1981). As the behavioristic taboos are relaxed or ignored, the ingenuity that has enabled psychologists to discover so much about learning and information processing can be redirected toward animals' subjective thoughts and feelings. This is a very hopeful prospect, and the chief barriers to its realization lie in the current mindset of many experimenters.

There is a significant, though still largely unrecognized, intellectual underworld of ethologists and psychologists who often suspect that their subjects could scarcely do what they do without some conscious thinking and subjective feeling about their situation and their efforts to solve problems. Hundreds of talented scientists are actively studying how animals solve problems, the extent to which they deal in generalizations and concepts, and whether they employ simple plans or expectations. We can take full advantage of the rich body of data about animal problem solving under both natural and laboratory conditions, without being unduly troubled by the scientists' stated reasons for conducting their investigations. Even though semantic behaviorism still frowns on terms with mentalistic connotations, the results and interpretations of experiments are continually providing new and stronger evidence that animals sometimes think consciously (Honig and Thompson 1982). In short, while most of the scientists who study animal cognition deny any concern with animal consciousness, the fervor of these denials seems to be slowly waning.

Rats and other laboratory animals easily learn that a certain light or sound will be followed by an electric shock. They may cringe or show other signs of expecting the unpleasant shock before it is delivered. They can also learn how to prevent the shock by taking some specific action, such as moving to a different part of the cage or pressing a lever. After learning this so-called conditioned avoidance, the animal continues for long periods to react to the warning signal by taking the same avoidance action, even though it no longer receives any shocks (reviewed by Mackintosh 1974). It seems reasonable to conclude that the animal knows it will be hurt a few seconds after the warning signal un-

less it does what it has learned will prevent this unpleasant experience. But psychologists carefully avoid describing conditioned avoidance as evidence that the animal expects a painful shock following the warning signal and anticipates that it will be hurt unless it takes the avoidance action it has learned to be effective.

Many students of animal learning have noted that animals often act as though they are expecting something, and if it does not become available they appear surprised or disappointed. Tolman (1932, 1937) emphasized this sort of behavior in rats that were required to learn complex mazes in order to obtain food. In a typical experiment, after the rat had learned a moderately complex maze and was performing almost perfectly, choosing correctly a long series of right or left turns, the experimenter withheld the reward. On reaching the goal box and finding no reward, the rats would appear confused and search about for the food they had reason to expect.

One of the most dramatic examples is still one described by Tinklepaugh (1928, 224, also quoted in Tolman 1932, 75). He trained monkeys to watch the experimenter place a favorite item of food, such as a piece of banana, under one of two inverted cups that remained out of reach until a barrier was removed. The purpose of the experiment was to measure how long the monkey could remember which cup hid the piece of banana. When a monkey had learned to select the correct cup almost every time, provided it did not have to remember the situation for too long, the banana was replaced by lettuce during the short waiting period when the monkey could not see the cups or the experimenter. As Tinklepaugh described the results, the moderately hungry monkey now "rushes to the proper container and picks it up. She extends her hand to seize the food. But her hand drops to the floor without touching it. She looks at the lettuce but (unless very hungry) does not touch it. She looks around the cup . . . stands up and looks under and around her. She picks up the cup and examines it thoroughly inside and out. She has on occasion turned toward the observers present in the room and shrieked at them in apparent anger."

Numerous other experiments have confirmed Tolman's thesis that animals expect a particular outcome at certain times. For example, Capaldi, Nawrocki, and Verry (1983) have demonstrated that rats anticipate the patterns of reinforcement they have experienced in ways that support what they term "a cognitive view of anticipation." As summarized by Walker (1983): "Some kind of mental activity is being attributed to the animals: that is, there is considered to be some internal sifting and selection of information rather than simply the release of

responses by a certain set of environmental conditions. Knowledge of goals, knowledge of space, and knowledge of actions that may lead to goals seem to be independent, but can be fitted together by animals when the need arises" (p. 81). Naturalists and ethologists have gathered abundant evidence that such needs do arise very commonly in the natural lives of animals, and the resulting behavior strongly suggests that they understand in an elementary fashion what the problems are and how their behavior is likely to solve them. Animals appear to think in "if, then" terms. "If I dig here, I will find food," or "If I dive into my burrow, that creature won't hurt me." Likewise in the laboratory, "If I peck at that bright spot, I can get grain," or "If I press the lever, the floor won't hurt my feet."

A relatively simple case of expectation is demonstrated by the ability of numerous animals, including many invertebrates, to learn that food is available in a certain place at a certain time of day. They typically return to this place at or shortly before the appropriate hour on subsequent days and may continue, though with decreasing regularity, even after many days when no food has been found there. It seems reasonable to infer that these animals really do expect food at a certain time and place and that they experience disappointment, annoyance, or other subjective emotions when their expectations are not fulfilled.

There is also increasing evidence that many animals react not to stereotyped patterns of stimulation but to *objects* that they recognize despite wide variation in the detailed sensations transmitted to the central nervous system. As reviewed in chapter 3, a Thompson's gazelle recognizes a lion when it sees one. The lion's image may subtend a large or small visual angle on the retina, and it may fall anywhere within a wide visual field; the gazelle may see only a part of the lion from any angle of view. Yet to an alert tommy, a lion is a lion whether seen side or head on, whether distant or close, standing still or walking. Furthermore, its perceptions of lions are obviously separated into at least two categories: dangerous lions ready to attack, and others judged to be less dangerous on the basis of subtle cues not obvious to a human observer without considerable experience. Comparable behavior is so common and widespread among animals living under natural conditions that it seems not to call for any special scientific analysis. Yet the ability to abstract salient features from a complex pattern of stimulation, often involving more than one sense, requires a refined ability to sort and evaluate sensory information so that only particular combinations lead to the appropriate response.

Laboratory experiments on what is called reversal learning also sug-

gest conscious thinking. In a typical experiment of this type a rat is trained to recognize that a triangle marks the location of food but that an equally conspicuous circle does not. After the rat has been responding appropriately to these two stimuli quite accurately for some time, the experimenter suddenly changes the rules of the game, so that the circle now shows where food is available and the triangle yields nothing. In time the rat learns the reversed rules and again performs almost perfectly; it has changed its searching image from triangle to circle. But an interesting difference results from overtraining some rats on the first problem by letting them make the correct choice dozens or hundreds of times, while giving others just enough training that they have barely become proficient. One might expect that the overtrained rats would have the "triangle marks food" rule so thoroughly drilled into their brains that it would be more difficult to learn the reversed problem. But careful experiments have shown that under some conditions overtrained rats learn more easily than others to reverse their choice (Mackintosh 1974). Perhaps during the numerous reversals and relearning of rules in dozens of trials after the problem is initially solved, they begin to think consciously about the two patterns or even about the possibility of rule reversal and thus find it easier to grasp the new relationship. No one can say for sure, but communication with rats via such reversal learning experiments might be telling us something important.

Mackintosh (1974) and Walker (1983) have reviewed several other types of experiments showing that laboratory animals can learn relatively abstract rules, such as oddity or the difference between a regular and an irregular pattern. In oddity experiments the animal is presented with a number of stimuli or objects, one of which differs from the others in some way; it must learn to distinguish this "oddball" from the other members of the set. For many animals, learning a single case of this sort is not difficult. Chimpanzees, however, have learned to generalize oddity as such, and having learned to select a red disk placed with two blue disks, and a blue disk accompanied by two reds, they also selected the oddball when it was a triangle with two squares. Pigeons have much greater difficulty with comparable problems, but, surprisingly, they do better than cats and raccoons.

Variations on this experimental theme have led to other unexpected results. For instance, Zentall and colleagues (1980) compared the performance of pigeons faced with two types of oddity problem. In one case the birds saw a five-by-five array of twenty-five disks, one of which differed in color from the remaining twenty-four. In the other problem there were three only disks in a row, two alike and the third a different

color. In that case, if the positions of the odd-colored disk was varied randomly, or if the actual colors were changed, for instance from one green and two reds to two greens and one red, the pigeons failed to solve the problem. But with the array of twenty-five they quickly learned to peck at the disk that differed from the rest in color, even when the colors were shifted randomly from twenty-four reds plus one green to twenty-four greens and one red.

In a related type of experiment, Delius and Habers (1978) trained pigeons to distinguish pairs of visual patterns according to their relative symmetry or asymmetry. Having learned this task, they were also able to make the correct distinction on the first try when given new pairs of shapes, some of which were symmetrical and others not. Bowman and Sutherland (1970) trained goldfish to distinguish between a perfect square and one with a bump in the top edge. In one of many variations, goldfish that were trained to swim toward a square having a small triangular extension from its top, rather than a perfect square, also selected a circle with a small semicircular indentation in the upper edge in preference to a plain circle. They seemed to have learned to distinguish simple shapes from the same shape complicated by either an indentation or outward bulge. Walker (1983) expressed surprise that “even a vertebrate as small and psychologically insignificant as a goldfish appears to subject visual information to such varied levels of analysis.” Why should this be surprising, when it is well known that fish can discriminate many types of pattern that signal food or danger? We should be on guard against the feeling that only primates, or only mammals and birds, have the capacity for learning moderately complex discriminations. For the natural life of almost any active animal requires it to discriminate among a wide variety of objects and to decide that some are edible, others dangerous, and so forth.

### Life in the Skinner Box

Many laboratory studies of learning and discrimination between stimuli employ the Skinner box, in which a very hungry animal, typically a rat or pigeon, is isolated from almost all stimuli except those under study. To obtain food the animal must manipulate something in the box when a particular stimulus is presented to it. Opaque walls prevent it from seeing anything outside the box; and a broadband hissing noise is often provided to mask any outside sounds. Thus the animal has almost nothing to do but operate devices within the box that were originally selected because they were things that members of its species easily learn

to manipulate. For rats this is a lever close to the floor which they can depress with one forepaw, and for pigeons it is a key, or small back-lighted piece of translucent material flush with the wall at a height easily reached by the bird's beak. A third fixture of the Skinner box is a mechanically operated food hopper which provides access to food, or sometimes water, but ordinarily only for a few seconds at a time. Both levers and backlighted keys are attached to microswitches connected so as to control the food hopper or produce changes in the stimuli presented to the animal. General illumination in the box is also provided; and since pigeons rely heavily on vision, turning off this "house light" tends to inhibit most activities including key pecking.

Studies of learning in Skinner boxes have ordinarily been conducted and analyzed in strictly behavioristic terms; but some of the results provide significant though limited evidence about what the rats or pigeons may be thinking as they work for food or water. The most revealing evidence of this type has been obtained with pigeons, which rely much more than rats on vision. This facilitates complex types of experimental stimulation, that we, as equally visual animals, can more easily appreciate. Psychologists who study this sort of learning emphasize what they call contingencies of reinforcement, that is, the rules relating what the apparatus does in response to the animal's bar pressing or key pecking. A very simple rule would be for the food hopper to make food accessible for a few seconds whenever a pigeon pecks the key. Or the bird may be obliged to deliver two, ten, or some other number of pecks to obtain food. An early discovery in this type of investigation was that animals work harder if the food hopper operates only occasionally after a variable and unpredictable number of pecks or bar presses. This variable ratio reinforcement elicits a very high and sustained rate of responding. In this situation the hungry pigeon might think something like: "Pecking that bright spot sometimes gets me food, but not always. It's easy—almost like picking up seeds—so I'll keep trying until every now and then that box clanks and I can get some food."

In these experiments, pigeons are ordinarily deprived of food or water long enough to make them very hungry or thirsty; a standard procedure is to hold the bird's weight at 80 percent or even 70 percent of what it would be with food available at all times. When first put into a Skinner box most hungry or thirsty pigeons peck the key before too long; after all there is nothing else to do, and pecking is a natural action for hungry pigeons which pick up seeds or other small objects as a routine part of their daily lives. The new, learned behavior is to peck at the bright spot on the wall instead of an actual bit of grain. Since this causes



the food hopper to open and gives the bird a chance to pick up edible seeds for a few seconds, it is not surprising that most pigeons soon learn the basic rules of the game.

After this stage has been attained, the experimenter may change the rules so that the food hopper operates only some of the time, or only when some other information is supplied. One or more additional keys may be provided and their microswitches connected to circuits that operate the food hopper only when this key is lighted. The pigeons then learn to peck much more often when this second light is on, though they usually try occasional pecks at the food-getting key at other times as well, perhaps thinking that it might still work. Or the apparatus may provide food only when a certain color or a specific pattern is displayed, and endless variations on this theme have been used to measure sensory capacities and the ability to discriminate between similar stimuli.

These procedures were originally developed by psychologists who denied any interest in whatever subjective, conscious thoughts or feelings their experimental animals might experience. They had been conditioned by the intellectual *Zeitgeist* of behaviorism to restrict their concern to overtly observable behavior and how it could be altered by learning. Indeed one of the main advantages of the Skinner box is that the animal's behavior can be recorded mechanically and objectively as numbers and rates of bar pressing or key pecking. Any other behavior is ordinarily ignored, and the opaque walls of the Skinner box prevent the experimenter from seeing what else the animal may be doing. The psychologists who conduct these experiments almost never speak of the animals in Skinner boxes as hungry: they are food deprived, or maintained at 80 percent of free feeding weight. And they never let themselves be caught saying, in print, that such a pigeon might *want* the food-hopper to open or *believe* that pecking the key will get the food it must crave. When the animal learns to do what gets it food or water, such behavior is said to be "reinforced," rather than rewarded. This choice of terms reflects the behavioristic insistence on ignoring any mental experiences of the experimental subjects.

Once we allow ourselves to escape from what the philosopher Daniel Dennett (1983) called "the straitjacket of behaviorism," we can ask ourselves what it may be like to be famished or very thirsty in a closed box where a little food or water can be obtained by playing the Skinner box game. Consider a typical experiment where the box contains two back-lighted panels in addition to the white key that sometimes, but not always, activates the food hopper. One panel is red when turned on, the other green, and the food hopper operates occasionally when the red

light is on, but never with the green panel illuminated. A plausible inference is that the pigeon might think something like: "When that spot is red I can sometimes get food by pecking the white spot." But how can we test such an inference? Perhaps it is quite wrong; the bird may be thinking about something entirely different, such as the perch where he spent last night, or the hen he was courting when last given an opportunity to do so. Or perhaps he does not think about anything at all.

Straub and Terrace (1981) trained pigeons to peck at colored keys in the wall of the Skinner box and to do so while following a particular sequence of colors. To get its food, one pigeon might have to peck first red, then blue, yellow, and green, while another was required to peck in the sequence yellow, red, green, blue. These pigeons were faced with two rows of three spots that could be illuminated with different colors. In the most significant experiments four of the six spots were illuminated simultaneously, each one a different color, but the positions of the colors varied from trial to trial; the pigeon had to ignore the position of the spots and select the appropriate colors in the correct sequence in order to obtain food. Several pigeons solved this problem and performed at a level far above chance, indicating that they had learned a sequential rule that guided their decisions about which spot to peck. It seems plausible that they thought something like: "I must peck first at red, wherever it is, then blue, next yellow and then green."

One set of experiments with pigeons in Skinner boxes has provided a significant though incomplete indication of what the birds were thinking about. Jenkins and Moore (1973) departed from custom by actually watching what their pigeons were doing. They expanded upon earlier observations by Squier (1969) that fish "reacted to response keys with species-specific feeding movements" and the report by Wolin (1968) that "the form of the pigeon's operant key-contact response depends on the nature of the reinforcer." Close observation and photography showed that when pecking a food-getting key, pigeons held their bills in a position closely resembling that used in picking up actual seeds. But thirsty pigeons held and moved their bills in ways that were much like drinking. (Pigeons swallow water with a distinct set of movements that differ from those used to swallow seeds.) To avoid observer bias and expectations, ten judges who did not know whether the birds were hungry or thirsty, or whether they were rewarded with food or water, were shown motion pictures or video tapes of pigeons pecking keys in a Skinner box. Eighty-seven percent of their judgments were correct, and two of the judges made no errors at all. As summarized by Jenkins and Moore, "the basis for judgement most commonly mentioned was that

eating-like movements were sharp, vigorous pecks at the key. In contrast, the drinking like movements, it was said, involved slower, more sustained contacts with the key (or other object) and were often accompanied by swallowing movements.”

Later investigations have confirmed and extended these results. LaMon and Zeigler (1988) have reported detailed measurements of the pigeon's behavior when pecking at a key located on the floor of the Skinner box, and when actually taking grain or water. The most obvious difference between key pecks for food and water was that the beak was opened much farther for food reinforced keypecks (about 5.5 mm compared to 0.4 mm). Whether pecking the key or actually eating and drinking, the hungry pigeons used brief pecks with a relatively high force, while thirsty pigeons employed sustained contact movements of the head and beak. Although the scientific papers describing these experiments are constrained into orthodox behavioristic terminology, it is clear that hungry pigeons peck the key as though eating, thirsty birds as though drinking. Since food and water were of the utmost importance to these birds, it seems quite reasonable to infer that they were thinking about eating or drinking when operating the Skinner box mechanism to satisfy their hunger or thirst.

In another series of experiments Richard Herrnstein and several other psychologists have presented pigeons with truly challenging problems of memory and perception. In a pioneering experiment by Herrnstein and Loveland (1964) the standard Skinner box was modified so that in addition to the customary food-getting key there was a small screen flush with the wall on which colored slides could be projected. The screen also served as a key which closed an electrical switch when the pigeon pecked it. A wide variety of photographs were projected on this miniature screen, indoor and outdoor scenes, pictures of people, animals, buildings, trees, flowers, and street scenes. In all these experiments some slides, designated positive, signaled the availability of food; pecking them sometimes caused the food hopper to open for a few seconds. Other pictures, termed negative, were not reinforced; pecking them had no effect, or it might turn off the “house lights,” leaving the pigeon in darkness.

When the pigeons had learned to peck much more frequently at the positive pictures, the rules of the game were made even more challenging. They were now shown a large number of miscellaneous scenes, and key pecking obtained food only when the picture included a person or part of a human figure. All other pictures were unrewarded or negative. The positive pictures might show men, women, or children; the human

figure might be large or small, dressed in different sorts of clothing or engaged in a variety of activities, sitting, standing, walking, with or without other people or animals present. In some pictures only part of a human figure such as the face was included. The negative pictures varied just as widely. When pigeons were pecking significantly more often when shown pictures containing people, a series of wholly new positive and negative pictures were shown, ones that varied as much as the original set but which the birds had never seen before. Surprisingly, some of the pigeons mastered this task and pecked significantly more at the new pictures containing people. It is important to appreciate that the pigeons do not perform perfectly in these tests; typically they may peck at perhaps 70 to 80 percent of the positive pictures and only 20 to 30 percent of the negatives. But the numbers of pictures used in such experiments are so great that these differences are extremely unlikely to occur by chance.

Herrnstein termed this concept learning, for the pigeons had learned not specific pictures or patterns, but categories. In other experiments of the same general type pigeons learned to distinguish: (1) oak leaves from leaves of other trees (Cerella 1979), (2) scenes with or without trees, (3) scenes with or without bodies of water, (4) pictures showing a particular person from others with no people or different individuals (Herrnstein, Loveland, and Cable 1976), and (5) underwater scenes containing fish as contrasted with similar underwater pictures containing no fish (Herrnstein and de Villiers 1980). This last task was selected because pigeons would never in their individual or species experience be obliged to discriminate among underwater scenes.

In other experiments by Poole and Lander (1971) pigeons learned to distinguish pictures of pigeons from other animals and birds. After having been trained with positive photographs of normal pigeons they treated as "pigeon" pictures of "weird" pigeons described as "fancy varieties having heavily feathered feet, abnormal head, body, or tail structures." This suggests recognition of a variety of pigeons as something equivalent to "one of us," although it has not been demonstrated that pigeons can learn more easily to recognize pictures of pigeons than other animals such as dogs or hawks. It is important to bear in mind that in all cases the crucial tests were carried out with brand new pictures, never shown to the pigeons before. Herrnstein et al. (1989) trained pigeons to follow "an abstract relational rule" by pecking at patterns in which one object was inside, rather than outside of a closed linear figure. Herrnstein (1984, 1990) does not claim that these concepts are equivalent to the rich meaning conveyed by words in human

language, but some elementary classification of very diverse scenes is clearly accomplished by the pigeons.

This type of experiment has been further elaborated recently by Wright, Cook, Rivera, Sands, and Delius (1988) to test whether pigeons could master the concept of same versus different. In several previous experiments, pigeons had failed to make this distinction in a reliable and convincing fashion. Wright et al. developed a modified Skinner box in which three pictures  $5 \times 6$  cm in size were projected side by side on the floor instead of the wall of the Skinner box. The pictures were cartoons produced by a computer graphics program. When the pigeon pecked at the correct picture a simple mechanism dispensed seeds directly on the screen where the picture was projected; thus the association of a given picture with food was closer than in the standard Skinner box. In each trial three pictures were projected on the three screens, and either the righthand or the lefthand picture was identical to the central one. If the pigeon had grasped the rule that the correct picture to peck was the one that was the same as the middle picture, it should perform correctly when presented with wholly new sets of pictures.

Two pigeons were trained by repeated trials with two cartoons—a duck and an apple. Sometimes the duck was the central picture and at other times the apple, and the matching picture varied irregularly in position, left or right. After 1,216 presentations during seventy-six trials, the pigeons were making the correct choice 75 percent of the time. But when tested with new sets of pictures they performed only at the chance level. It proved very difficult to train these birds to make the correct choices with a third and fourth set of pictures even after many sessions. Two other pigeons were shown 152 different sets of pictures in each day's testing session, and each picture was shown only once in the seventy-six trials. Learning was slow and uncertain, but after 360 training sessions over eighteen months they were making 75 percent correct choices. When these pigeons were presented with new sets of pictures, however, they did slightly better, 83 percent correct. Evidently the lengthy training with 152 sets of pictures had enabled the pigeons to recognize that the correct picture, whatever its nature, was the one that matched the central image. Wright et al. (1988) conclude that "the ability to learn a concept (same-as-the-center-picture), however, does not mean that this is the pigeon's preferred learning strategy. Quite the contrary, it is clear from the vast amount of research with pigeons that they prefer to attend to absolute stimulus properties and to form item-specific associations."

It is interesting that this problem of matching to a sample seems

much more difficult for a pigeon than selecting pictures containing a certain feature such as a tree, person, or fish when the actual appearance of these objects varies enormously in prominence and other attributes. Distinctions that seem elementary to us may not be at all obvious to another species. And, conversely, tasks such as recognizing an important class of object even when it differs widely in size and other attributes is probably of crucial importance in identifying edible foods or detecting dangerous predators at a sufficient distance to permit successful escape. Noticing which two of three objects are the same does not have any particular salience in the real world, where animals live under natural conditions. But learning to recognize some category of important objects such as food or predators is often a matter of life and death. When a new type of food becomes available, it is important for many animals to recognize it whenever possible without expending enormous time and effort trying and rejecting a huge range of objects. The same consideration is even more important with respect to dangers. A similar situation is indicated by the experiments of Roberts and Mazmanian (1988), who found that pigeons could more easily distinguish one kind of bird from another than make more general distinctions such as birds versus other kinds of animal. The results of these experiments make excellent sense from the perspective of a naturalist. Experiments on animal learning will probably become more significant when they employ stimuli and discriminations comparable to those that are important in the natural lives of the animals concerned.

It seems reasonable to suppose that when the pigeons are working hard in Skinner boxes to solve these challenging problems, they are thinking something like: "Pecking that thing gets me food"; that is, it seems most plausible to suppose that they classify things simply as those that do and don't produce food. In any event, it is difficult to imagine learning to solve such problems without at least basic and elementary perceptual consciousness. To be sure, strict behaviorists reject any such interpretation, and insist that it is unscientific to speculate about even the simplest sort of subjective thoughts of other species. While we cannot prove conclusively whether or not a pigeon making these categorical discriminations thinks consciously about the pictures or the features that lead it to peck or not, its brain must, at the very least, classify complex visual stimuli into one of two categories.

These experiments stimulated a number of further investigations, because they demonstrated that pigeons could learn not only specific stimuli but general categories. The basic finding has been replicated in other laboratories using somewhat different procedures. For example Siegel

and Honig (1970) repeated the Herrnstein and Loveland experiment using a Skinner box but varying the procedure by either showing the positive and negative pictures (with and without people) simultaneously on adjacent parts of the screen or sequentially, as in the original experiments. Again the pigeons transferred their discrimination to brand new examples, and they performed above chance levels when the pictures were upside down and when the negative pictures were photographs of the same scene as the positives but without a human figure.

In another replication Malott and Siddall (1972) used a modification of the Wisconsin General Test Apparatus developed for training monkeys and other animals to discriminate among various objects. The pigeons poked their heads through an opening in the wooden box where they were confined, and looked at two wooden cubes. On the faces of the cubes visible to the bird were glued colored photographs clipped from an illustrated magazine. When the bird pecked at a positive picture containing people, the cube was pulled away, uncovering a shallow well containing a kernel of corn; pecking negative cubes with miscellaneous pictures of geometric shapes, machinery, landscape, furniture, or animals yielded no food. Each positive picture was presented until the pigeon had made five consecutive correct choices, and then two new picture cubes were presented. After somewhere between three and seventeen such problems had been solved, the pigeons very seldom pecked at cubes with negative pictures that contained no human figures. Then, in the critical tests, wholly novel pairs of pictures of the same general sort were presented, and the pigeons performed almost perfectly.

These results were so surprising to those who had tended to view pigeons as stupid “learning machines” that alternative, simpler interpretations have been advanced to explain these findings. Many psychologists have been reluctant to agree with Herrnstein that pigeons can learn a concept. Yet something in the pigeon’s brain must correspond at least roughly to what we call the concept of person, tree, or fish. In a review of animal cognition, Premack (1983a, 358–59) expressed frustration because of “the inability of the reader (of these papers)—who is shown only a few of the test photographs—to judge for himself the author’s claim that the concepts could not be formed on the basis of ‘simple features.’” Premack had “never found this claim entirely convincing. Pigeons have never been shown to have functional classes—furniture, toys, candy, sports equipment—where class members do not look alike; they only recognize physical classes—trees, humans, birds—where class members do look alike.” But in many of these experiments the examples

of positive and negative categories did not look very much alike, and from the pigeon's point of view they did fall into two functional categories—those that yielded food and those that did not.

Lea (1984) doubtless spoke for many psychologists when he worried about just what we mean by acquisition of a concept, and whether the experiments of Herrnstein and others suffice to show that these birds have the concept of person, tree, or whatever object was present in a variety of forms in the positive pictures at which they learned to peck more often than at negative pictures lacking such objects. He and others seem to agree that the best definition of concept recognition, in contrast to learning to respond to a stimulus attribute such as color or shape, is that recognition of a concept can only be inferred "when there is no simple single perceptual feature on which a discrimination could be based." This definition is unsatisfying because it rests on a negative criterion, and proving negatives is notoriously difficult; strictly speaking, it is impossible. Thus one can always postulate that some simple feature that has escaped the notice of the investigators but has been recognized by the pigeons as a signal meaning "pecking that gets me food." But this idea avoids granting that pigeons can understand simple concepts only by postulating a literally "superhuman" ability to discern some simple but single feature that is present in the positive but not the negative pictures.

Another complication in interpreting these experiments stems from the remarkable ability of pigeons to learn and remember hundreds of specific pictures, and to respond appropriately to most of those that yielded food even weeks or months after they were last seen (Skinner 1960; Greene 1983; Vaughan and Greene 1984). For instance Wilkie, Wilson, and Kardal (1989) have trained pigeons to recognize airplane views of a particular geographical location. Other birds have comparable abilities, as demonstrated, for example, by the experiments reviewed by Balda and Turek (1984) showing that Clark's nutcrackers remember where they have stored hundreds of seeds. But the ability of pigeons to respond correctly to most if not all of *new* positive or negative pictures they have never seen before rules out an explanation based on a simple memory of specific pictures.

As might be expected, behavioristic psychologists have been very reluctant to interpret these experiments as evidence that pigeons might think consciously about the categories that they learn to distinguish. For example Premack (1983a) describes experiments by Epstein, Lanza, and Skinner (1980) in the following terms: "The basic approach has been to find performances in apes or monkeys that are recom-



mended as proofs of mind and then demonstrate the same performance in the pigeon. Although this could backfire (and be taken as showing mind in the pigeon) . . . the opposite conclusion is drawn: what need is there for mind when there are contingencies and reinforcement?" In this exchange Epstein and his associates were expressing doubt that experiments on self-recognition by chimpanzees (discussed in chapter 12) demonstrate that they had minds, using as an argument the fact that somewhat similar performances could be elicited from pigeons by means of operant conditioning, apparently taking it for granted that pigeons are mindless. Premack's use of the term "backfire" captures nicely the widespread reluctance of psychologists to credit even as complex animals as pigeons with any sort of mental experience.

A recent extension of the pioneering experiments of Herrnstein and Loveland has strengthened the case for something approaching the conscious awareness of simple concepts or categories, although, to judge by some of their other publications, the psychologists who conducted the experiments would probably dispute this interpretation of their findings, as discussed below. E. A. Wasserman and several colleagues trained pigeons to recognize and distinguish four categories simultaneously (Bhatt, Wasserman, Reynolds, and Knauss 1988; Wasserman, Kiedinger, and Bhatt 1988). Their apparatus and procedures are of interest, because they provide additional hints about how the situation may appear to the pigeons. The Skinner box was provided with a  $7 \times 7$  cm viewing screen and four circular keys 1.9 cm in diameter and located 2.3 cm diagonally from the four corners of the picture screen. When activated, these keys differed in color. In preliminary training the pigeons learned to get access to food by pecking first the picture screen and then whichever one of the colored corner keys was illuminated. At this stage the picture screen was a uniform white.

After this task had been mastered, the pigeons were presented every day with a series of forty pictures, ten of which included a cat, ten a flower, ten an automobile, and the other ten a chair. As in earlier experiments of this type, the pictures varied widely in content and the cats, flowers, autos, and chairs also varied widely in size, color, and position in the picture. Along with these pictures all four of the corner lights were turned on, and the pigeon was required to peck a different corner light if the slide on the central screen contained a cat, a flower, an automobile, or a chair. The pigeons obtained food only if they first pecked at the picture about thirty times and then pecked at the correct one of the four colored keys. Only this key activated the food hopper and provided something for the hungry bird to eat.

Initially the pigeons had no way of knowing these rather complicated rules of the Skinner box game, and they were equally likely to peck at any one of the four corner keys, so that their choices were correct only about one quarter of the time. Every day the pigeons were given forty trials, ten with each type of picture, and after ten days they were performing better than chance. By thirty days they were making, on average, 76 percent correct choices. By this time they had had ample opportunity to learn all forty pictures, each of which they had seen thirty times. Since pigeons can learn and remember dozens or hundreds of pictures and identify at far better than chance levels those that get them food, at this point the experiment had only shown that pigeons can learn four sets of pictures at the same time and respond to them by pecking the correct one of the four colored keys. The critical stage of the experiment consisted of mixing in among the ten familiar pictures of each type entirely new and different pictures containing one of the four key features. The pigeons still made primarily the right choices, although they were correct a somewhat smaller fraction of the time. But they did generalize to new examples of these four types of picture at much better than chance levels. In another experiment of the same type the pigeons learned to classify stimuli into four types without ever seeing the same slide twice.

In later experiments Wasserman and his colleagues (in preparation) have trained pigeons to discriminate between pictures of human faces expressing strong emotions such as anger or sadness. The pigeons responded correctly at better than chance levels to new pictures of different persons displaying the same emotions. Of course, the training could not teach the birds anything about the emotions of the people photographed when sad or angry. But these experiments do show that fairly subtle categories of visual patterns can be learned by birds. This ability probably stems from the very widespread need to evaluate the likelihood that a predator will attack or that a given spot is or is not something edible.

Wasserman and his colleagues conclude from these and many related findings that "the conceptual abilities of pigeons are more advanced than hitherto suspected" (Bhatt et al. 1988, 219), and that "these results suggest that many words in our language denote clusters of related visual stimuli which pigeons also see as highly similar. To the degree that reinforcement contingencies correlate with these human language groupings, pigeons' discrimination learning is hastened and generalization to new and altered examples is enhanced" (Wasserman, Kiedinger, and Bhatt 1988, 235). In keeping with the behavioristic tradition, the

papers describing these impressive achievements of pigeons are titled "Conceptual Behavior in Pigeons." Presumably this wording was chosen to reinforce the behavioristic insistence that any mental terms be scrupulously avoided. Animals may behave as though they utilized simple concepts, but behaviorists are constrained to ignore or deny the possibility that they might consciously think about the categories or concepts that must be postulated in order to explain their behavior.

It is significant that Wasserman (1981, 1982, 1983, 1984, 1985) has argued vigorously in favor of the behavioristic taboo against any implication of consciousness despite the recent revival of research on animal cognition to which he has made important contributions. For example: "I, for one, have tried to steer clear of the possibility of subjective experience in my animal subjects; the more prudent of my professional colleagues have as well; . . . cognitive psychology need not be construed as mentalistic. Those cognitive processes that are said to mediate behavioral relationships are the public behaviors of scientists, not the private experiences of their subjects" (Wasserman 1983, 10–11). And, more recently: "No statement concerning consciousness in animals is open to verification and experiment. Isn't it time we set aside such tantalizing, but unanswerable, questions and direct our energies to more productive pursuits?" (Wasserman 1985). Perhaps as psychologists come to recognize such similarities between human and animal cognition, they will gradually begin to suspect that human and nonhuman mental experiences may also have much in common.

In a few special situations animals give evidence of thinking in terms of simple concepts such as numbers or even names of individuals. The German ethologist Otto Koehler and his colleagues at Freiburg in southwestern Germany carried out numerous experiments on the abilities of birds to solve problems that required what he called "wordless thinking," meaning that they thought about objects and relationships but not in terms of words (Koehler 1956a, 1956b, 1969). In one of the most impressive of these experiments, birds were trained to select from a number of covered vessels the one having a certain number of spots on the lid. The spots varied in size, shape, and position, but a well-trained raven could reliably select the pot with any number from one to seven spots.

From the results of many such experiments Koehler concluded that these birds had the concept of numbers from two to seven, which he called unnamed numbers. This ability may be comparable in some ways to the very earliest stages of understanding of numbers in preverbal children (Gelman and Gallistel 1978). Koehler also believed that animals

understand other relatively simple concepts as unnamed thoughts. There is little reason to suppose that thinking about unnamed numbers had been useful enough in the past for natural selection to have favored it specifically. Yet when it became important to think in this way to get food, ravens and a few other birds learned to do so, apparently employing general ability to learn simple concepts. To be sure, Seibt (1982) has argued that since pigeons can learn as easily to peck three times when shown two lighted spots as to peck twice when shown three, there is no basis for the claim that birds have an unnamed number concept in the sense claimed by Koehler. But these data can just as easily be interpreted by crediting pigeons with the ability to learn two correlated unnamed numbers, that of the stimulus and that of the required response.

Davis and Memmott (1982) have pointed out that although several birds and mammals have been able to learn to count in the sense of responding selectively to different numbers of objects, this is a relatively unnatural sort of behavior that has only been elicited by "relatively extreme experimental conditions." Capaldi and Miller (1988a, 1988b) and Davis, Mackenzie, and Morrison (1989) have demonstrated that rats are capable of a simple form of discriminating what is sometimes called "numerosity" to distinguish it from the sort of counting by mentally assigning successive numbers as we usually do. Numerosity is a rudimentary type of concept that lies within the capabilities of at least some birds and mammals.

Hediger (1968, 1976) has reviewed evidence that many mammals can recognize their names when these are used by zoo keepers. Of course, domestic animals and pets routinely learn to come when called by the names given them by their human owners. Hediger suspected that certain animals had "unnamed names" for other animals and for familiar human companions. But although many animals undoubtedly recognize individually other members of their species, there is no convincing evidence that one animal addresses another by some individual name, although the recent investigations of Tyack discussed in chapter 11 suggest that the individual-specific "signature whistles" of dolphins might be used as something roughly equivalent of names for familiar companions.

Davis (1989) has reported that rats learned that they could obtain food in a certain situation, but only when the experimenter was not present to prevent them from obtaining it. The rats came to refrain from efforts to reach the food when the experimenter was present but took it when he was absent. They had thus learned that the presence of an object quite different from the food meant they would be prevented from

obtaining it. This is so simple a relationship that it scarcely deserves to be called a concept, but it is an example of the sorts of contingencies that animals often learn.

The directional orientation of honeybees provides further examples of moderately complex integration of information derived in different ways and at different times. Many of the relevant experiments have been conducted by Dyer and Gould (1981), and by Gould (1980, 1982, 1986, 1990), and the general subject has been reviewed by Gould and Gould (1988), Gould and Towne (1988), and Gallistel (1990). Many of these experiments were possible only because honeybees employ a symbolic communication system, discussed in detail in chapter 9, that allows them to convey to their sisters (and to eavesdropping ethologists) the direction in which a desirable source of food is located. Ordinarily this direction is indicated relative to the azimuth direction of the sun. This of course changes during the day, and if bees are prevented from communicating about a desirable food source for some time, they indicate not the direction in which the food was located when they visited it, but a different direction that results from at least a rough compensation for the sun's apparent change in direction. The rate of change in sun azimuth varies considerably with season, latitude, and time of day, so that bees face a problem in achieving this compensation. The results of experiments reported by Gould (1980) indicate that the compensation is probably based on the rate at which the sun's azimuth was changing when the bee flew to and from the food source.

When the sky is completely overcast, bees still communicate the direction in which they must fly to reach it, at least under some conditions. Earlier experiments reviewed by von Frisch (1967) indicated that bees remember the food location with reference to landmarks. But Gould (1981) found that after displacement to a new location under a completely overcast sky their directional communication is still expressed relative to the sun even when this direction must be remembered. Furthermore, this memory must include at least an approximate compensation for the time of day. This sort of directional communication cannot help to recruit completely naive bees, but in many cases the active foragers from a particular colony are likely to be familiar with major local landmarks, so that the information that food is available in a particular direction can presumably be interpreted as meaning to fly along a conspicuous linear landmark such as the edge of a wooded area bounding an open field.

In later experiments, Gould (1986) observed the flight directions of bees captured as they left the hive to return to a desirable food source

that they had been visiting for some time. They were carried in dark closed boxes to another location, released, and their initial flight directions observed. The hive, the food site, and the experimental release point were located at the apices of an equilateral triangle, so that the direct route from the new location to the food source was 60 degrees different from the original flight direction from hive to food. Most of the bees started in this new direction, and to judge by the time needed to reach the food they flew quite directly. This experiment was repeated with similar results at hive-to-food distances of 160 and 350 meters, and with the location of food source and release point interchanged, so that the new direction of flight deviated from the normal hive-to-food direction by 60 degrees clockwise and counterclockwise. But when the bees were carried 4,425 meters away, they departed randomly in a wide variety of directions, as would be expected since it is rare for honeybees to forage this far from their hive. Gould interprets these data as demonstrating that honeybees employ what are called "cognitive maps," that is, they have some sort of internal representation of the geometrical relationships of important objects and major landmarks, and use this to orient their flight when displaced to a novel location within the area with which they are familiar. Similar experiments with rats and other vertebrates have been carried out by Tolman and others, but insects had not been believed capable of this level of cognition.

Menzel (1989), Menzel et al. (1990), Wehner and Menzel (1990), Wehner and Wehner (1990), Wehner et al. (1990), and Dyer (1991) have conducted similar experiments with honeybees but the results have indicated direct orientation toward familiar landmarks rather than the use of cognitive maps. Gould (1990) has presented evidence that in his experiments the local terrain did not provide specific landmarks that were within the resolution of honeybee pattern vision. Perhaps differences in local topography or in the experience of the bees underly this difference in experimental results. At present the question remains an open one, and further experiments are needed to clarify the situation. But whether or not honeybees are capable of using cognitive maps, they are certainly able to integrate more than one type of sensory input and stored patterns in determining in which direction to fly.

Another sort of evidence suggesting that honeybees may think in terms of concepts such as the nature of flowers and where within a flower the nectar is to be obtained has been reviewed by Gould (1979, 1982). Human agriculture often presents honeybees with challenging problems. The anthers of alfalfa flowers spring back vigorously at a visiting insect, thus dusting it with pollen. These flowers are adapted for

pollination by larger insects such as bumblebees. When honeybees enter them they are knocked about so violently that they learn very quickly to avoid alfalfa. But when no other flowers are available, honeybees learn to enter only alfalfa flowers whose anthers have already been tripped by another insect, or, when the colony is in extreme need of food, they bite a hole in the back of the alfalfa flowers to reach the nectar. This atypical method is also used in other situations, as reviewed by Inouye (1983).

A final thought-provoking type of behavior that suggests conceptual thinking has been observed by several investigators of the symbolic communication of honeybees that will be discussed in chapter 9. To observe communication about distant resources, investigators must induce bees to visit controlled food sources at distances of several hundred meters. To accomplish this, often in the face of serious competition for the bees' attention from natural flowers, a concentrated sugar solution is first provided in a small dish right at the hive entrance. After many bees have begun to gather sugar solution from such a feeder it is gradually moved farther and farther from the hive. At first it can be moved only a few centimeters, later a meter or so, without losing the bees. But when it is about 30 meters from the hive, the experimenter can move it by much larger jumps, and the same bees return to it after carrying stomachs full of sugar to their sisters in the hive. When the feeder is more than 100 or 200 meters from the hive, it can be moved 20 or 30 meters at a time, and many bees that have visited it at previous locations begin to search for it beyond where they found it last. They seem to have realized that this splendid new food source moves, and that to find it again they should fly farther out from home. If so, they may be thinking in terms of the simple but abstract concept of a moving food source.

There is some doubt whether this conclusion is justified by the available evidence, for adequate experiments have not yet been reported that would rule out other interpretations, such as a tendency to scatter in all directions around the former location of the food, so that a few bees would happen to arrive at its new location. Nevertheless this possibility deserves further investigation, because if bees do extrapolate the position of food sources in such a situation, this ability would represent an unusually enterprising versatility of behavior and perhaps of conscious thinking. Of course, real flowers do not ordinarily move 20 or 30 meters in a few minutes, so that it is difficult to imagine how natural selection would have prepared honeybees to extrapolate the position of a moving feeder. Yet one can imagine natural situations where something similar could occur. Near steep mountain ridges the area of morning sunshine gradually expands as the mountain's shadow diminishes. The

area where flowers open and make nectar available may expand with the sunlight under some such conditions, so that a similar extrapolation of expected food locations might be advantageous. Perhaps the repertoire of genetically programmed foraging tactics encoded in honeybee DNA provides for this special situation. But even if we accept this rather far-fetched explanation, we must still credit the bees with adapting a tactic ordinarily used in the early morning near steep mountains to flat terrain and to other times of day.



## *Physiological Indices of Thinking*

**T**aking it for granted that both behavior and conscious thinking result from the functioning of brains or central nervous systems, we may appropriately inquire whether the extensive studies of brain function have provided any evidence concerning the particular processes that produce conscious thought. Although a thorough review of the cognitive neurosciences is far beyond the scope of this book, a few especially salient experiments provide significant evidence that conscious thinking is not a monopoly of our species, or even of our close relatives. John (in Thatcher and John 1977), among others, has equated consciousness with a sort of internal feedback whereby information about one part of a pattern of information flow acts on another part. This may be a necessary condition for conscious thinking, but it is not sufficient, for it is also an aspect of many physiological processes that operate without any conscious awareness on our part.

Human speech depends heavily on certain areas of the temporal cortex (principally Broca's and Wernicke's areas); but this localization of function is not precise and absolute, for damage to particular parts of the speech control areas does not always produce the same effects, as reviewed by Lecours et al. (1984). Furthermore, as far as neuroanatomical evidence goes, these areas of the brain are not unique to our species. Homologues of Broca's and Wernicke's areas are present in other mammals, but they are not called by the same names since the animals are incapable of human speech. Nevertheless a few recent discoveries about brain mechanisms controlling communicative behavior in monkeys and birds do throw some light on these questions because these mechanisms share some properties with those that control human speech.

## Lateralization of Brain Mechanisms Controlling Communicative Signals

The investigation of animal communication discussed below in chapters 8 to 11 has yielded unexpected evidence that particular species are so constituted that specific types of sounds or other signals are much more important to them than other physically comparable signals. In a few cases this has led to the processing of such important types of signal being concentrated in one side of the brain. This is best known in the case of human speech, and indeed it was argued until quite recently that lateralization of speech control, ordinarily in the left temporal cortex, was a qualitatively unique human attribute and formed a physiological basis for our vastly superior mental abilities based on language. But this all-or-nothing dichotomy is no longer tenable, because several cases have been discovered in which animal brains also concentrate the processing of communicative signals in one side of the brain. The clearest example is the lateralization of control of singing in songbirds, which also shows other intriguing parallels to lateralization of human speech control (Nottebohm 1979; Konishi 1985; Arnold and Bolger 1985; McCasland 1987).

Other instances of lateral specialization of brain mechanisms for the control of communicative signals have recently been discovered in monkeys. One of the clearest has been demonstrated by Hamilton and Vermeire (1988), who studied twenty-five monkeys (*Macaca mulatta*) in which the corpus callosum connecting the two cerebral hemispheres had been surgically cut. In such animals, or in human patients whose corpus callosum has been cut in order to control severe epilepsy, the two halves of the brain operate more or less separately. In these twenty-five monkeys the hippocampal and anterior commissures and the optic chiasm were also cut in the midline, thus separating the two sides of the cerebral cortex more completely than in many other "split brain" experiments of this general type. The monkeys had recovered fully and behaved quite normally except that when allowed to see things with only one eye, only one cerebral cortex received visual input. This allowed the experimenters to train them to make various visual discriminations separately with either the right or the left cortex. When required to discriminate between straight lines differing in slope by 15 degrees, the monkeys performed significantly better when using the left hemisphere. But when the problem was to discriminate between pictures of the faces of individual monkeys, the right cortex was superior. These differences were quantitative and not absolute; both hemispheres could learn to

perform both discriminations, but the superiority was clear and statistically significant.

The recognition that primate vocalizations conveyed specific information in addition to levels of emotional arousal began with very detailed studies by Green (1975) of the sounds exchanged by Japanese macaques (*Macaca fuscata*) in relatively relaxed social situations. He found that a group of sounds most readily described as "coos" differed in acoustical details, even though they had at first seemed much the same to human listeners. Furthermore certain types of coo-like sounds were used most often in specific situations. For example, "smooth early highs," which began at a fairly high frequency, rose slightly, and then declined in pitch, were usually emitted by infants sitting apart from their mothers. On the other hand, "smooth late highs," in which the frequency rose steadily to peak near the end of the call before dropping slightly, were most often used by sexually receptive females. This and other observations indicated that these cooing sounds were especially important in the social communication of Japanese macaques. This led Zoloth and Green (1979) to suggest similarities to human speech.

The coos are not the only vocalizations used by Japanese macaques to communicate with their social companions when they are close together and interacting amiably. Another type of sound, called "girneys" by Green, have been studied in detail by Masataka (1989). These are sounds with multiple harmonics that rise in frequency and fall toward the end of each vocalization. Masataka distinguished two general sorts of girney, those in which the peak frequency occurred during the first third of the sound, and others that peaked in the final third. The first type was often followed by the caller grooming the receiver, while the latter type usually resulted in the receiver grooming the caller. Thus these two types of sound seem to mean something like "I'll groom you," and "Groom me." This interpretation was supported by the results of playbacks of tape-recorded sounds, which were followed by motions and gestures that strongly indicated that the hearer expected to be groomed or to groom the companion nearby. This is an additional example of the subtle differences in animal signals that used to seem meaningless but have been shown by careful experiments to convey different messages.

Building on these findings, Zoloth et al. (1979) trained Japanese macaques and three other species of monkeys to discriminate between tape-recorded coos on the basis of two acoustic features. The first was the position of the frequency peak, early or late in the sound, which seems to convey different meanings to the Japanese macaques, and the

second was the frequency at which the coo began. One of the other species, the vervet monkey *Cercopithecus aethiops*, does not use coos in its social communication; the other two do have coo-like sounds, but it is not known whether they have any special significance to the animals themselves. The Japanese macaques consistently learned the discrimination of peak position more easily than the other three species, but they were poorer at learning to discriminate on the basis of the initial frequency. Thus the perceptual capabilities of these species of monkeys appeared to be correlated with the acoustic features of the sounds they use for social communication.

In related experiments these coo-like sounds were presented to Japanese macaques and to five other species of monkeys through earphones that allowed the experimenters to present the stimuli to either the right or the left ear (Petersen et al. 1978, 1984). Since most of the auditory neurons of mammals cross the midline before reaching the cerebral cortex, a right ear advantage means that the left auditory cortex is playing a larger role than the right in processing such signals. When sounds are presented to the human right ear, we can usually discriminate small differences better than with sounds arriving at the left ear.

All five Japanese macaques showed a significant right ear advantage for detecting the position of the frequency peak, while only one of the other monkeys showed this effect. When the monkeys' task was to make discriminations based on the initial frequency of the sound, one Japanese macaque showed a left ear advantage, while another monkey of this species and two of other species showed no difference between the two ears. It is important to recognize that these right or left ear advantages are not absolute; the monkeys and human listeners can make the discriminations with either ear, but more often perform better when the sound is delivered to one of the two ears. This evidence that Japanese macaques, but not the other species tested, process coos primarily with their left auditory cortex was further supported by the experiments of Heffner and Heffner (1984), who trained animals to make the same discrimination between coos on the basis of the position of the peak frequency. Then parts of the brain were surgically removed, and after recovery the monkeys were tested again in the same way.

When the auditory cortex on both sides of the brain was removed, the monkeys could no longer make this discrimination even after additional training. But they performed normally when only the right auditory cortex was removed. After the left auditory cortex had been destroyed, the monkeys' performance was initially poor; but with further training it improved and reached its former level. Evidently these mon-

keys had been using the left auditory cortex before the operation but could relearn the discrimination with the right cortex when necessary. This result is intriguingly similar to the localization of human speech perception in the left auditory cortex, more specifically in Wernicke's area.

These experiments indicate that recognition of at least one type of sound used in social communication is concentrated on one side of the brain in one species of monkey. Lateralization of speech perception and control used to be considered a unique brain mechanism underlying human speech and thought. The finding of similar lateralization in songbirds and in Japanese macaques is reminiscent of the nineteenth-century controversy between Owen and Huxley over the former's claim that there was no hippocampus in the brains of nonhuman primates. Human mental superiority, enormous as it is, does not seem to be based on any single, unique feature of neuroanatomy.

Recent technical developments have allowed noninvasive procedures to depict which parts of a brain are most active, but these methods are complex and expensive and have so far been employed for the most part in human clinical investigations and diagnosis, as reviewed by Posner et al. (1988) and Scheibel and Wechsler (1990). Kosslyn (1988) has reviewed evidence that both hemispheres of the human cortex are activated when subjects experience mental images—a clear example of how supposedly unobservable mental experiences can be studied. But most of these procedures are limited in spatial resolution, so that they would be difficult to employ with brains as small as those of many animals. In one important recent investigation, however, Georgopoulos et al. (1989) have recorded the action potentials of neurons in the motor cortex of a monkey while it moved a lever to follow the motion of a spot of light. The activity of these neurons occurred in the same spatial pattern as the hand motion that followed after a fraction of a second. This suggests that the monkey was perhaps thinking about the movement it was about to carry out. But the time interval by which this patterned activity of the motor cortex preceded the actual movement was a fraction of a second; so one could interpret these data as simply reflecting an early stage in the physiological process leading the monkey to move its hand as it had been trained to do.

A related area of exciting progress in neurophysiology is the identification of neurons that are selectively responsive to particular classes of stimuli. Monkeys recognize the faces of known companions, and can readily be trained to respond selectively to sketches of monkey faces (Dittrich 1990). Some neurons in the temporal cortex of monkeys re-

spond to pictures of faces, whether these be actual simian or human faces or pictures of them. The extensive literature on this sort of selective responsiveness has been reviewed by Maunsell and Newsome (1987), and representative recent experiments on face recognizing neurons is described and analyzed by Perrett, Rolls, and Caan (1982). Baylis, Rolls, and Leonard (1985) report evidence that some neurons are selectively sensitive to particular monkey faces. We do not know whether a monkey is more or less likely to be conscious of recognizing the face of a known companion when these neurons are active. But the fact that a central nervous system can be so organized that particular cells respond to very specific types of patterned stimuli does demonstrate what refined types of discrimination are possible for primate brains. It would be of great interest to carry out comparable experiments with other groups of animals, using patterned stimuli that are of special importance to them.

### Physiological Indices of Conscious Thinking

Inasmuch as cognition is obviously an active process carried out by central nervous systems, neurophysiologists attempting to understand brain function seek objective data that can be measured when brains are engaged in their complex and enormously significant activity. The principal data available are electrical potentials. These clearly accompany not only the conduction of impulses along neurons but the all-important modulating processes that occur at synapses. Ideally, a neurophysiologist prefers to record with microelectrodes from individual neurons or synapses, or at most a few at a time. But when dealing with the more complex and significant processes of cognition, monitoring the activities of single cells is clearly of limited use. This is because whatever activities of central nervous systems lead to cognition and conscious thinking require complex interactions of large numbers of cells.

One general type of electrical signal that can be recorded from central nervous systems reflects the massed activities of hundreds or thousands of neurons and synapses. Relatively weak electrical signals generally known as electroencephalograph (EEG) potentials, or, more popularly, as brain waves, can be recorded both from electrodes inside brain tissue and also from outside an animal or human skull. These EEG potentials have been recorded extensively from the human scalp and often give useful signs of clinical abnormalities. Neurophysiologists have been tempted from time to time to hope that with sufficiently detailed and ingenious analysis these signal might be correlated with specific cogni-

tive activities going on within the brain. These hopes have generally been disappointed, and the prevailing opinion of leading neurophysiologists is that EEG potentials are too coarse and too gross an index to reveal more than the most general sorts of activity. Nevertheless certain recent developments in the analysis of electrical potentials recorded from both human and animal brains offer a tantalizing suggestion that with much further refinement this approach might throw some light on the questions under consideration in this book.

First it will be necessary to digress briefly to emphasize that neurophysiologists are generally cautious scientists who refrain from interpreting their data beyond their immediate and clear-cut relevance to well-defined questions. Thus they almost never express any opinions about such elusive phenomena as conscious thinking, even though they are concerned with the neurophysiological mechanisms that are generally agreed to underlie all types of information processing, cognition, and even consciousness. Conscious thinking has simply appeared to be a slippery subject that is considered beyond the immediate reach of contemporary experimental analysis. But behind the respectability blanket of scientific caution, neurophysiologists dare to dream that their science is gradually building a foundation upon which an understanding of conscious thinking will eventually be attained. It is therefore necessary to extrapolate somewhat beyond the tangible evidence and stated conclusions in our attempt to discern how the neurophysiological mechanisms underlying conscious thinking may come to be understood.

The predominant EEG potentials recorded from an intact brain are of relatively low frequency. They are also ordinarily only a few microvolts when recorded from the human scalp. The most prominent are the alpha waves with a frequency on the order of 5 to 8 Hz that are most evident when the human subject is lying quietly with closed eyes and is not engaged in any particular mental activity. If the subject performs some mental task such as solving arithmetic problems, these alpha waves diminish in amplitude and merge into more irregular, noisy signals covering a broad frequency band. This is a disappointing fact for those who would hope to extract from the EEG signals a direct correlate with mental activity.

Nevertheless, one indication of localization of function has been obtained by analyzing EEG waves from the two sides of the human brain. While the electrical signals are present over both cerebral cortices, there are small quantitative differences when the subject engages in thinking about different types of subject matter. Verbal problems, such as selecting synonyms from a series of words, produce slightly larger potentials

over the left cerebral cortex, as one would expect from the well-known fact that the left side of the cortex is much more heavily involved in processing and recognizing speech. But this evidence does not add anything of great importance to what was already known from data on the effects of damage to different parts of the human brain.

Neurophysiologists have found that a different type of electrical potential can be recorded from the human scalp after discrete sensory stimulation such as flashes of light or brief sounds. Ordinarily these are too low in voltage to be detected reliably against the background of other EEG signals, but this difficulty has been surmounted by repeating such discrete stimuli and averaging the EEG potentials. Although this can be done by a variety of methods, the most convenient and effective procedure is to use a digital computer to average the potentials and display them graphically as a function of time after the presentation of the stimulus. Typically several hundred or even a few thousand stimuli must be averaged to obtain a clear graphic display, which sets obvious limits to the kinds of stimuli that can be studied. They must be brief—otherwise, excitation from a later part would complicate responses from the earlier portions—and they must be repeated many times.

These potentials resulting from discrete sensory stimulation are ordinarily called evoked potentials, and they are described in terms of electrical polarity and time or latency after the stimulus. Those portions of the evoked potentials occurring within less than about one-tenth of a second are clearly reflections of the sensory impulses traveling from the peripheral sense organs to successively more anterior portions of the brain. These are useful indices of sensory input but reveal relatively little about cognition, let alone consciousness.

A subset of evoked potentials, usually having longer latencies are clearly correlated with moderately complex information processing. There are tantalizing hints that under some conditions these may be related to decision making or other simple types of conscious thinking. They are usually called event related potentials, abbreviated ERPs, because they are not a direct function of the sensory input but are also affected by internal processes within the brain, including previous events.

There is an enormous literature describing a wide variety of event related potentials, and this discussion will concentrate only on a few of the more clear-cut types which provide significant suggestions about the occurrence of conscious thinking. Donchin et al. (1983), Picton and Stuss (1984), Stuss, Picton, and Cerri (1986) and Sommer, Matt, and Leuthold (1990) have reviewed the evidence relating these poten-



tials to human consciousness. The whole subject has been reviewed in two articles by Verleger (1988) and Donchin and Coles (1988) in the journal *Behavioral and Brain Sciences*, which also publishes numerous comments by other interested scientists and responses to these comments by the authors. Almost all of the papers and discussion of event related potentials has been concentrated on those recorded from human brains, but in a few experiments quite similar potentials have been recorded from the brains of laboratory animals, primarily cats and monkeys. To appreciate the significance of the latter potentials, it is necessary to review briefly the data from human subjects that point toward a correlation between ERPs and conscious thinking.

From a wide variety of components of ERPs, much of the experimental attention, and the most interesting implications, come from what is usually called the P300 wave. This is a positive potential occurring about 300 milliseconds after a stimulus. Actually it lasts in many cases 100–200 msec and the peak varies somewhat, but is ordinarily in the range of 300–400 msec. The defining characteristic of the P300 wave is not so much its electrical or temporal properties as its relationship to at least simple types of cognition.

One of the most widespread experiments suggesting this relationship involves presenting a long series of uniform stimuli, usually sounds, one of which is occasionally omitted. P300 waves occur after all of these sounds, but the one following the omission of an expectable signal is often as large or larger than those following actual stimulation. Since there was no stimulus at all preceding the P300 waves for an omitted stimulus, these waves must reflect some sort of activity in the brain related to the general pattern that had been established by the repeated stimuli. A somewhat similar experiment is to present a train of stimuli including two types, one much more common than the other. The relatively rare stimulus has come to be called the “oddball” stimulus. Under many conditions all stimuli produce P300 waves, but the oddball stimuli generate larger ones, as reviewed by Galambos and Hillyard (1981).

More closely related to possible thinking is a variation on this experiment in which the common and rare stimuli differ in semantic meaning. In one intriguing experiment of this type the subject heard the spoken name David 80 percent of the time and Nancy in the remaining 20 percent (Donchin 1981). In another experiment 80 percent of the names were masculine and 20 percent feminine. In still another variation on this experimental theme 20 percent of the words rhymed with cake and 80 percent did not. In a final experiment the oddballs were synonyms of prod and the others were not. The subject’s task was to

count the number of times the rare stimuli were heard. In all cases there were prominent P300 potentials, but the rare stimuli elicited, on the average, larger ones with longer latency. The difference in latency was greater when the subject's task concerned semantic meanings. It takes the brain longer to deal with the problem of deciding whether the sound was a word synonymous with "prod" or rhyming with "cake" than to simply distinguish between the common and the less common of two words.

Cautious neurophysiologists tend to limit their interpretations of such data to the conclusion that a substantial portion of the brain is active when responding to these stimuli and that the summated electrical effects or their time course differ when the response is more complicated. This is, at least, a significant opening, a sort of entering wedge that might lead to more detailed and significant analyses. It is therefore pertinent to inquire whether animal brains show comparable potentials. The answer is that those of cats and monkeys certainly do, although the detailed form of the ERPs may differ from the human P300 waves to some extent. Wilder, Farley, and Starr (1981), Buchwald and Squires (1982), and Harrison, Buchwald, and Kaga (1986) have recorded evoked potentials from cats which were very similar to the human P300. These electrical responses were prominent, however, only after either the brief tone or light flash had been associated with the delivery of an electrical shock to the cat's tail. In other words, the stimulus did not produce a significant P300 initially, but did so after the cat had been conditioned that it signaled an unpleasant event. In one experiment a cat learned that a light flickering at 7.7 times per second signaled that it would receive an electrical shock unless it made a simple response, but that 3.1 flashes per second meant it could obtain food. The ERPs increased in amplitude and changed their waveform after the cat had learned what to expect.

In a similar experiment with monkeys (*Macaca fascicularis*), two tones of 500 and 4,000 Hz were presented, the latter occurring less often than the former. The rare stimulus was accompanied by an electric shock. After the monkey learned that the rare tone would be followed by a shock, its brain showed a clear P300 wave in response to it but not to the other sound. Neville and Foote (1984), Glover et al. (1986) and Pineda et al. (1988) showed that in squirrel monkeys (*Saimiri sciures*) an oddball tone elicited a larger P300 wave.

These and other comparable experiments showed that the brains of cats and monkeys give long latency positive waves similar to the human P300 in their correlation with the novelty and meaningfulness of the

stimulation. This can be interpreted conservatively as showing only that meaningful stimuli activate larger numbers of neurons and synapses in both human and animal brains, which is scarcely surprising since the animals clearly learn to respond appropriately to stimuli they have learned have a particular significance. The behavioristic interpretation of these data is simply that the experiments have monitored electrical activity correlated with information processing, but that this tells us absolutely nothing about the presence or absence of conscious thinking. Nevertheless, as the functioning of some animal brains is found to resemble to a greater degree the comparable functions in human brains, the possibility of conscious awareness certainly does not diminish. It is therefore appropriate to consider what is known about the relationship between the human P300 wave and the conscious thinking that can be reported by human subjects.

Sommer, Matt, and Leuthold (1990) found that conscious expectations modified the human P300 to some extent, although the subjects were not conscious of most of the factors affecting these event related potentials. Donchin et al. (1983) addressed this question directly, accepting verbal reports as relevant objective data about the conscious experiences of human subjects. While there is a rough correlation between the presence of a P300 wave and the subject's awareness of the stimulus, the two do not always occur together. Some P300 waves have been recorded following stimuli that the subjects did not consciously notice, and the absence of P300 waves has been recorded following stimuli the subjects did notice. Given the complications of recording P300 waves and the numerous other electrical events that often obscure them, the occasional mismatch between their occurrence and conscious awareness of the stimulus is not altogether surprising.

The general conclusion, after many detailed studies of human P300 waves, is that they are endogenous in the sense that they are not direct results of stimulation. They are elicited by stimuli that are unexpected and yet are relevant, stimuli that signal something important, whether pleasant or unpleasant, or signals informing the subject of something he or she is expected to do. This has led to the general interpretation that the P300 results from an updating of the internal representation of some important aspect of the subject's situation. When the process of updating is more complex, there tends to be an increase in the P300 latency, but this is not invariable. Donchin et al. (1983, 112) concluded that "a consideration of the circumstances in which the P300 component is observed suggests that whenever P300 occurs, the subject is conscious of the task-relevant information carried by the eliciting stimulus.

In this sense, P300 can be used to index the occurrence of conscious processing." Nevertheless, there are exceptions, and the presence of a P300 wave does not demonstrate with absolute certainty that the human subject is aware of the stimuli. Verleger (1989) and Donchin and Coles (1988) and numerous commentators on these two papers debate at length and in almost excruciating detail just what these potentials reveal about the activities of the human brain.

Despite such uncertainties, the presence of an electrical potential that correlates with task relevance and the unexpectedness of stimuli is at least suggestive evidence that the subject is consciously thinking about the meaning of the stimuli. The requirement that stimuli must be repeated many times in order to measure ERPs means that only certain types of situation can be studied in this way. But it does seem that ERPs from animal brains deserve much more intensive study than has yet been reported. It would be of great interest to arrange experiments in which the stimuli had clear semantic meanings or required that animals make important decisions on the basis of information thereby conveyed. Certain types of ERPs may be necessary though not sufficient for conscious thinking; and their occurrence, magnitude, latency, and correlation with relevance to the animal might provide very helpful indications of the likelihood that it was indeed thinking consciously about the information conveyed by the experimental stimuli.

The reluctance of behavioral scientists to become enmeshed in the complicated problems of consciousness may have discouraged attempts to study experimentally the correlation between human conscious awareness and ERPs recorded from the human scalp. It would seem possible to arrange conditions under which human subjects made the same or very similar discriminative responses to stimuli that produce ERPs but did so under two sorts of conditions, one in which they were clearly aware, consciously, of their responses and the other in which they were not. The avoidance of conscious awareness might be achieved through long repetition and overlearning, or by distraction of competing stimuli. But experiments of this type do not seem to have been carried out with the care and ingenuity required. Thus we do not yet have more than rather general and uncertain correlations between human ERPs and conscious awareness. We should not, however, be discouraged from further experimental investigation of ERPs from animal brains when the animals are engaged in discriminations that are important to them and that might plausibly be supposed to be accompanied by conscious thinking.

## *Communication as Evidence of Thinking*

**I**t is much more effective for one animal to anticipate another's actions than to wait until they are underway. This is especially obvious in the case of aggressive encounters. When a dominant animal signals its intention to attack it is much better for a subordinate to perceive this as a threat than to wait until it is actually injured. For threats can be dealt with in several ways, including retreat, counterthreats that may deter the attack, or submissive behavior. Insofar as animals ever experience conscious thoughts and feelings, these are very likely to accompany social behavior and interactions between predators and prey. Many, if not most interactions between animals may well involve at least simple feelings and thoughts about the situation. If so, other animals with which signals are exchanged will benefit by correctly understanding what the communicator feels or wants, as emphasized by Krebs and Dawkins (1984). Communication is often a two-way process, a repeated exchange of signals by which two or more animals can perhaps evaluate each other's feelings and thoughts as well as their likelihood of behaving in various ways.

Animal communication can therefore provide a useful and significant "window" on animal minds, that is, a source of objective evidence about the thoughts and feelings that have previously seemed so inaccessible to scientific investigation. Experimental playbacks of communicative signals are of crucial importance because they allow a limited but revealing sort of participatory dialog between animal and scientist. Sounds are the most easily simulated signals, but other sensory channels can also be employed in playback experiments provided only that technical means are available to reproduce the animal signal with adequate fidelity. This has even been effective with electric fish, which use weak electric signals not only for orientation but in social and predator-prey interactions (Bullock and Heiligenberg 1986; Kramer 1990).

The implications of this general proposition that animal communi-

cation provides objective, verifiable data on animal feelings and thoughts are so far-reaching and so significant for cognitive ethology that they call for thoughtful consideration. Ethologists seldom inquire whether an animal may want or intend to attack, or whether another may fear injury. But if we recognize that such basic subjective feelings and thoughts may occur in animals, we can often make much better, and more parsimonious, sense out of their behavior. Russell (1935) in a thoughtful discussion of the basic challenges of investigating animal mentality concluded that "perception or imagery which does not issue in action must remain unknown to us, unless of course the subject can in some way communicate such perceptions and images to us." This is just what communicative behavior may sometimes do. Yet psychologists have paid little attention to the communicative behavior of animals, for reasons that are not entirely clear. Could this lack of interest stem from the pervasive inhibitions of behaviorism for the very reason that communication does suggest thinking?

One reason that has discouraged ethologists from using the communicative behavior of animals as a source of evidence about their feelings and thoughts is a conviction that all animal communication is a direct result of internal physiological states that are not under any sort of conscious control. Animal communication is thus held to be comparable to human eye blinks, blushing, gasps of surprise, or groans of pain. These do of course serve to communicate to others the state of irritation of the eye, embarrassment, surprise, or pain. But they are not intentional signaling employed for some perceived purpose. I have called this general view of animal communication the "groans of pain" or GOP interpretation (Griffin 1985). A related view is that threats are not signals that an animal wants or intends to attack but predictive information that leads to an appropriate response on the part of the animal that is threatened. This viewpoint considers animals to be simple-minded "behaviorists" who care only about what other animals do. On the other hand, insofar as conscious thoughts and subjective feelings affect subsequent behavior, it must be more efficient for both sender and receiver to recognize them by means of communicative signals that report them.

How can we hope to tell whether a given sort of communicative behavior does or does not fall into this GOP category? One important indication is the effect of an audience. Since GOPs are assumed to depend directly on some internal physiological state, it should not matter whether any other animal is present. Eyelids blink when the cornea is irritated regardless of any audience. But the communicative signals of many social animals are often dependent on the presence of other ani-

mals, and they are often modified in response to communicative signals received from others, as discussed below. The important basic point is that reasonable and appropriate interpretation of communicative signals exchanged by animals may provide significant though not conclusive evidence about their thoughts and feelings. Analysis of this evidence can, at the very least, provide an entering wedge into what has previously been held to be inaccessible territory beyond the reach of scientific investigation.

### Semantic Alarm Calls

One of the clearest examples of natural animal communication that suggests conscious thinking stems from studies of the alarm calls and other vocalizations of vervet monkeys (*Cercopithecus aethiops*). These monkeys, about the size of a small dog, live both in forests and in open areas of Africa where they can be observed more easily. They spend most of their lives in stable groups consisting mostly of close relatives, who recognize each other as individuals. When they see dangerous predators they emit at least three types of alarm call, originally described by Struhsaker (1967). One type is elicited by the sight of a leopard or other large carnivorous mammal. One of the few flying predators that preys on vervets, the martial eagle, calls forth an acoustically quite different alarm call. And when the monkeys see a python they give a third call that is clearly different from the other two.

This differentiation of alarm calls according to the type of danger leads to clearly distinct responses. The immediate response to the leopard alarm call is to climb into a tree; and since leopards are good climbers, monkeys can best escape from them by climbing out onto the smallest branches. But this would make them vulnerable to a martial eagle, and the response to eagle alarm calls is to move into thick vegetation close to a tree trunk or at ground level where they would not be at all safe from a leopard. In response to the snake alarm call, the vervets simply stand on their hind legs and look around at the ground. Once they can see a snake they can easily run away from it, although pythons do take vervets by surprise. Thus the best ways to escape from the three principal predators of these monkeys are mutually exclusive, and it is very important that the alarm calls inform other members of the group *which* danger threatens. A generalized escape response would be inefficient; there is no need wasting time climbing into a tree if the danger is from a python, and mistaking a martial eagle for a leopard or vice versa could easily cause the monkeys to do just the wrong thing.

Although it is clearly advantageous for vervet alarm calls to convey the information that one of the three types of predator had been sighted, many scientists did not accept the differences in the alarm calls as proof that an animal can convey semantic information about the nature of the danger rather than merely its state of fear or arousal. For example, Montagna (1976) stated, "With one cry, the monkeys take to the ground; with another, they climb trees; but in neither case do they know what predator they are escaping from." Vervet monkeys are ordinarily close to each other, and their first response to an alarm call is to look at the caller. Like many other animals they are adept at judging the direction in which a companion is looking, so that they can usually see for themselves what has caused the alarm and respond appropriately. Also the caller is likely to flee from the danger quickly, so that the other monkeys might simply do what he is doing. In view of the deep-seated conviction that animal communication could not convey semantic information, it had seemed more parsimonious to interpret Struhsaker's observations as evidence that the three alarm calls conveyed only the degree of fear, or that they were a scale of intensity rather than having specific meanings about the nature of the threat. Yet the three calls vary in intensity with the degree of the caller's arousal, so that this interpretation seemed somewhat strained.

Carefully controlled experiments by Robert Seyfarth, Dorothy Cheney Seyfarth, and Peter Marler (1980) resolved this uncertainty. The first step was to become so thoroughly familiar with groups of vervets living under natural conditions in East Africa that all individuals could be recognized. The next was to habituate the monkeys to the presence of human observers and their recording equipment. Then they played back alarm calls that had previously been tape recorded when a member of the group had first seen a predator. Many precautions were necessary to obtain convincing data. The monkeys might well respond abnormally, if at all, to playbacks of a known companion's alarm calls when he was in plain view and obviously not frightened. Therefore the loudspeaker had to be concealed in vegetation, and since monkeys recognize the calls of individual group members, playbacks were attempted only when the monkey whose calls were to be reproduced had just moved out of sight of his companions into the general vicinity of the concealed speaker, when the monkeys were not actively engaged in other behavior, and when they were not reacting to real dangers. Their behavior before, during, and after the playbacks was recorded by means of motion pictures, and the evaluation of responses was made by observers who viewed the films without knowing what call had been played.



These playbacks elicited the appropriate responses in most cases. The vervets climbed into trees on hearing playbacks of leopard alarm calls, and dove into thick bushes in response to the eagle alarm calls. Playbacks of the snake alarm call caused them to stand on their hind legs and look all around for a nonexistent snake. Somewhat similar results have been reported for lemurs by Macedonia (1990) and Pereira and Macedonia (1991). Yet many inclusive behaviorists remain reluctant to accept the straightforward interpretation that these three types of alarm call convey information about the type of predator the caller has seen. One alternative is that the alarm calls are injunctions rather than statements about the kind of danger. The leopard alarm calls might mean something like "Go climb a tree," the snake alarm call "Stand up and look around," and so forth. Even this somewhat strained interpretation recognizes that the calls are more than expressions of arousal. Their meaning might be what to do, rather than what danger threatens, but such injunctions are also semantic messages.

Vervet monkeys emit many other types of sounds during their social interactions. Cheney and Seyfarth (1982) have analyzed by experimental playbacks, comparable to their studies of alarm calls, the "low-pitched, pulsatile grunt, originally described by Struhsaker (1967) . . . given in a variety of social contexts." To human listeners these grunts seem rather nondescript sounds, and like many other animal sounds they were commonly interpreted as a graded series conveying only some emotional state of arousal. Close analysis of their acoustic properties showed very slight differences that could be distinguished by human listeners only after considerable practice. When different responses to grunts were observed, it had been customary to assume that this was due to differences in the situation or context in which an essentially unitary type of sound was emitted. Cheney and Seyfarth suspected, however, that subtle differences among the grunts might be recognized by the monkeys as conveying different meanings. Unlike predator alarm calls, grunts did not elicit any vigorous responses from other vervets, except that they often looked at the companion who grunted.

In planning their experiments, Cheney and Seyfarth reasoned that "if the grunts were really one vocalization whose meaning was largely determined by context, subjects should show no consistent differences in response to the calls. Instead, responses to playback should be a function of the variable contexts in which they were presented. On the other hand, if each of these grunts was different, and if each carried a specific meaning, we should expect consistent differences in responses to each grunt type, regardless of the varying circumstances in which they were

played." They therefore selected recordings of grunts emitted in five different social contexts, using only cases when they had been able to record all the interactions that preceded and followed the vocalization. Only grunts of each type that were similar in duration and amplitude were used for playbacks, and grunts that were responses to other grunts were excluded. Numerous playbacks were made of grunts to a dominant male, to a dominant female, to subordinate females, to a monkey moving into an open area, and to another group of vervet monkeys.

The monkeys showed some revealing differences in their responses to these playbacks of grunts. One of the clearest differences was that grunts directed at dominants caused none of twelve monkeys hearing the playback to move away from the loudspeaker; they apparently conveyed an appeasing rather than a threatening message. But grunts to subordinates produced movements away from the speaker in five out of twelve cases. The vervets spent more time looking towards the speaker after playbacks of grunts to dominants than grunts emitted on seeing a monkey move into the open, and there were similar quantitative differences between some of the other types of grunts used in these experiments. Although these experiments do not indicate just what meaning the grunts conveyed, they do show that they were not interchangeable. As summarized by Seyfarth (1984), "When a monkey hears a grunt, he is immediately informed of many of the fine details of the social behavior going on, even though he may be out of sight of the vocalizer, and even though the vocalizer himself may not be involved."

In other recent investigations Seyfarth (1987) and Cheney and Seyfarth (1990) used selective habituation of responses to repeated playbacks of vervet calls to learn something of their meaning to the monkeys themselves. They concentrated on three calls given only in the presence of another group of vervets: a grunt, a chatter, and a call designated *wrr*. Playbacks of any of them caused the monkeys to orient towards the signaler and to look in the same direction as the signaler. When such playbacks were repeated in the absence of another group, the duration of these responses gradually diminished. After such habituation had occurred to repeated playbacks of the *wrrs* of a particular monkey, not only his *wrrs* but also his intergroup chatters elicited a much weaker response. Yet when the same experiment was repeated using the *wrrs* or chatters of another monkey, this elicited a normal intensity of response.

In other words the monkeys tended to ignore both the type of intergroup vocalization that had been repeated without the presence of another group, and the acoustically different sound used by the same monkey that presumably conveyed the same or a similar meaning. Thus the

habituation was specific to the individual caller, regardless of the category of call used by that animal. The vervets seemed to recognize that if one type of intergroup call by a given companion had proved inappropriate, his other intergroup calls also deserved less attention. On the other hand, when the same experiment was repeated with alarm calls elicited by leopards or martial eagles the result was significantly different. Although the vervets did habituate to the groundless leopard alarm calls of a particular companion, played back from a tape recorder, they still responded to playbacks of the eagle alarm calls of that individual. It seems likely that predator alarm calls are such serious matters that the monkeys cannot afford to ignore them even when the caller has previously "cried wolf" about a different type of danger.

### Semantic Screams

Another type of semantic information conveyed by animal calls is the social relationship between the caller and another member of the group to which he belongs. This has been most clearly demonstrated in studies of the free-ranging rhesus macaques (*Macaca mulatta*) that have been studied for many years on Cayo Santiago Island off Puerto Rico. When these and other monkeys engage in aggressive encounters, they often call loudly, and this calling sometimes serves to enlist the aid of others against the antagonist. Gouzoules, Gouzoules, and Marler (1984) selected a well-studied group of these monkeys for detailed studies of the screams given by immature males when exchanging threats or fighting with other members of the group. These monkeys could all be recognized individually, and both their maternal ancestry and social status was known from extensive previous studies. It was thus possible to distinguish whether a young male was interacting with a close relative or not, and whether his opponent was higher or lower in dominance rank. The screams of these young males often brought the screamer's mother to his aid.

Many previous studies of monkeys' calls had indicated that they varied continuously in their acoustic properties. This has been interpreted as a fundamental difference between monkey calls and human language, because the latter consists of discrete words while animal calls have been viewed as merely emotional signals devoid of any meaning except to convey the state of arousal of the caller. It was therefore a surprise to find that 90 percent of 561 recordings of the agonistic screams of these juvenile males fell into one of five distinct categories. On the basis of sound spectrograms these five categories were desig-

nated as noisy, arched, tonal, pulsed, and undulating screams. The noisy screams had a broad frequency spectrum from about 2 to 5 kHz. Arched screams had narrow frequency bands which rose and fell one or more times. Tonal screams had a wavering but gradually descending frequency from about 5 or 6 to 2 or 3 kHz. Pulsed screams were similar to noisy screams but broken up into pulses each lasting only about 0.1 second. Finally, the undulating screams consisted of a series of four or five harmonics which wavered up and down several times during a duration of roughly 0.7 to 1.2 seconds. Although these screams varied considerably in detail, these five categories could easily be distinguished by human listeners.

These screams tended strongly to be used selectively toward different categories of opponent. With some exceptions, noisy screams were directed at higher-ranking adversaries when there was physical contact—including biting. Arched screams were given almost exclusively to lower-ranking opponents when no physical contact was taking place. Both tonal and pulsed screams tended to be given more often to relatives of the caller, while undulating screams were directed almost entirely to higher-ranking opponents when no physical contact was involved. Thus the screams contained information about the severity of the encounter and the social status of the opponent.

The mothers of callers also responded differently to these screams, as demonstrated by playbacks of tape recordings. The basic procedures employed in these playback experiments were the same as those used by Seyfarth, Cheney, and Marler in the experiments with vervet monkey alarm calls. The first response of the mothers was to look towards the concealed loudspeaker; they did so for 100 percent of the noisy screams given to higher-ranking opponents with physical contact, but less consistently in response to the other types. The duration of their gaze towards the speaker was much longer for noisy and arched screams than for tonal and pulsed screams, and they reacted more quickly to these types than to the others. The responses of mothers to screams that were repeated for several seconds included threat displays and charging from a considerable distance uttering loud calls of their own.

In other experiments the same investigators found that mothers respond more strongly to the screams of their own sons than to those of other young males (Gouzoules, Gouzoules, and Marler 1986). Similar studies of a large group of captive pigtail macaques (*Macaca nemestrina*) by Gouzoules and Gouzoules (1989) showed that in this species different types of screams were emitted when fighting or threatening opponents of different social rank. But screams of pigtail macaques did not

seem to differ according to matrilineal relatedness, as they did with rhesus monkeys.

The results of these investigations show that the screams of these monkeys, unlike groans of pain, convey considerable information about the caller's situation, information that affected their mothers' behavior. It seems likely that the monkeys think about these highly emotional situations in simple terms of the degree of threat and danger and the social relationships of the opponent or, in the case of the mother, of their offspring's situation.

### Audience Effects

As mentioned above, one way in which ethologists might be able to distinguish communicative signals that do or do not fall into the "groans of pain" category is to study the effect of an audience on the production of communicative signals. Marler and his colleagues have been attempting to do this with the calls emitted by domestic chickens. Chickens emit a wide variety of calls, as described by Collias and Joos (1953) and Collias (1987), and they are of course convenient animals to study. Marler and his colleagues concentrated on two types of call given by adult males of a small strain, the golden Sebright bantam, that seems to be quite similar to the ancestral jungle fowl from which domestic chickens derived. Because some of the most interesting calls are rather faint, they were recorded by temporarily attaching to a cockerel's back a  $2 \times 2.5 \times 5$  cm radio microphone weighing 16 grams. The birds became accustomed to wearing these instruments and their behavior did not seem to be appreciably altered by them.

Chickens, like several other species of birds, have two types of alarm calls, a series of short, narrow band whistles commonly given when they see aerial predators such as hawks, and a pulsed broad-band cackle elicited by ground predators such as dogs or foxes. But the type of danger is not the only factor affecting which call is produced, so that they are not a highly specific form of signal. The so-called ground predator call is also given to hawks at close quarters, and the aerial alarm call is often given to small and harmless birds or other objects seen against the sky. Yet despite much variability and many calls given when the observers could detect no danger or other appropriate stimulus, there is nevertheless a strong tendency for the aerial alarm calls to be given for hawk-like objects seen in the sky and the ground predator alarm call for moving objects at ground level.

Marler and his colleagues arranged conditions in which a single ban-

tam cockerel lived for long periods in a large outdoor cage. Models of hawks were presented by pulling them along overhead wires, much as Lorenz and Tinbergen had done in their classic studies of avian responses to hawk-like patterns. Under these conditions the cockerels emitted 509 aerial alarm calls in 400 presentations of moving hawk models, but no ground alarm calls at all (Marler, Dufty, and Pickert 1986a, 1986b; Gyger, Marler, and Pickert 1987; Karakashian, Gyger, and Marler 1988; and Marler, Karakashian, and Gyger 1991). The cockerels gave significantly fewer aerial alarm calls when alone than when their mate or another familiar female was clearly visible and audible in an adjacent cage; but when this experiment was repeated with unfamiliar females the male called no more often than when he was alone. Familiar males elicited almost as many alarm calls as familiar females. Young chicks were almost as effective an audience as familiar females in eliciting alarm calls, but the presence of bobwhite quail did not increase the frequency of alarm calling. Evans and Marler (1991) have recently refined these experiments by showing that video tapes with sound tracks have the same effects as live birds. This allows improved experiments in which possibly confounding effects, such as variation in activity of the quail and chicken could be experimentally controlled.

Cockerels also give other calls when food becomes available, and in the experiments they called more when presented with preferred foods such as mealworms or peas than for peanuts or inedible nutshells. Females approached males giving these food calls more than noncalling males, and they were more likely to approach a male calling about a preferred food. Males also called more when hens were present, and hardly at all when another adult male was in the adjacent cage. This is doubtless related to the fact that courting cockerels often bring food to females in which they are interested. The amount of food calling by the males also varied with the nature of the conspecific audience. When no other chickens were present, males gave food calls 13 out of 18 times that mealworms were presented, and only once in 18 presentations of inedible nutshells. When another male was present, they gave no food calls at all for either mealworms or nutshells, although they ate 15 of the 18 mealworms. When either familiar or unfamiliar females were present, the cockerels never ate the mealworms and gave food calls in 35 of 36 presentations. Thus the presence and nature of an audience had a marked effect on food calling.

It is significant that these audience effects are different for food calls and alarm calls. Almost as many alarm calls were given in the presence of familiar males as familiar females, but no food calls at all were given

to males. Although Marler et al. are cautious about interpreting these data, and carefully consider other factors that might cause the differences they observed, their experiments certainly support the hypothesis that cockerels are appropriately selective about their use of both alarm calls and food calls according to the nature of their audience. To be sure, other considerations such as the whole context in which communication takes place are also important in interpreting these experiments, as discussed in detail by Smith (1991). But, at the very least, the experiments demonstrate that as more is learned about communicative behavior of animals, it becomes increasingly difficult to fit such behavior into the procrustian bed of GOPs.

## Honeyguides

An intriguing type of foraging that suggests intentional planning and communication of simple thoughts is the guiding behavior of the African greater honeyguide (*Indicator indicator*). These birds feed on insects but are also fond of the wax from honeycombs, and they are able to digest beeswax. They cannot open bee nests, but in an apparent effort to obtain wax and honey they cooperate with men or perhaps animals that tear open bee nests to take honey, leaving a considerable amount of honeycomb available to the honeyguides. The several species of honeyguides and their behavior were studied intensively by the ornithologist Herbert Friedmann and described in his 1955 monograph. His analysis of the cooperative behavior is significant as a classic example of the reductionistic *Zeitgeist* that was so prominent in studies of animal behavior for many decades and led even the most experienced field naturalists to underestimate the versatility of the animals they studied. More recently Short and Horne (1985) have thoroughly investigated the behavior and ecology of honeyguides with special emphasis on their roles as nest parasites that lay their eggs in the nests of other species. The following review of honeyguide behavior is based on Friedmann's monograph, substantially supplemented (and in important respects modified) by the recent work of Short and Horne, and especially that of Isack and Reyer (1989) discussed in detail below.

Honeyguides are widely believed to lead the ratel or honey-badger (*Mellivora capensis*) to bees' nests. They also engage in the same sort of cooperative behavior with people, and in some areas African natives seek out honeyguides to obtain honey from the nests of wild bees. Some, according to Friedmann, imitate the grunting sounds of ratels, or chop on trees to simulate the sound of opening a bees' nest. Occa-

sionally a honeyguide has been reported attempting to lead a mon-goose, monkey, or baboon; but only baboons have been observed to follow the bird. Most of the detailed observations of the guiding behavior have involved human cooperators, and several recent students of honeyguides suspect that they never cooperated with ratels and that the idea they did so arose because the nocturnal ratels were seen feeding on honeycomb after it had been exposed by human honey gatherers.

Friedmann believed that the guiding habit had decreased markedly from earlier years as European ways of life have provided more easily obtained sources of sugar than the opening of wild bees' nests. He also suspected that ratels had become more nocturnal, under increased human hunting pressure, so that honeyguides had less opportunity to obtain wax by this type of cooperative behavior. The guiding behavior seems always to have been limited to certain areas within the honeyguide's range, so that it is far from being a rigidly fixed behavior pattern. Regardless of this question, there is no doubt that, in many areas of Africa, honeyguides lead human searchers for bees' nests to their location, and that after the honey gatherer has opened the nest the birds profit by obtaining honeycomb.

As Friedmann (1955, 32-33, 39-41) describes typical guiding behavior:

When the bird is ready to begin guiding it either comes to a person and starts a repetitive series of churring notes or it stays where it is and begins calling these notes and waits for the human to approach it more closely. . . . If the bird comes to a person to start leading him, it flies about within 15 to 50 feet from him, calling constantly, and fanning its tail, displaying the white outer rectrices. If it waits for the potential follower to approach it for the trip to begin, it usually perches on a fairly conspicuous branch, churring rapidly, fanning its tail, and slightly arching and ruffling its wings so that at times its yellow "shoulder" bands are visible. As the person comes to within 15 to 50 feet from it, the bird flies off with an initial conspicuous downward dip, with its lateral rectices widely spread, and then goes off to another tree, not necessarily in sight of the follower, in fact more often out of sight than not. Then it waits there, churring loudly until the follower again nears it, when the action is repeated. This goes on until the vicinity of a bees' nest is reached. Here the bird often (usually in my experience) suddenly ceases calling and perches quietly in a tree nearby . . . and there waits . . . until the person has departed with his loot of honeycomb, when it comes down to the plundered bees' nest and begins to feed on the bits of comb left strewn about. . . .

Guiding may cover a duration of from a few seconds to half an hour, or possibly even an hour, and may involve a distance of from a few feet to over half a mile, and possibly, at times, even a mile. . . . Guiding leads to the vicinity of a



bees' nest, not to the exact spot. . . . If a person does not follow a honey-guide that has apparently come to "lead" him, the bird may increase the tempo and excitement of its behavior as if to urge and entice, or it may give up easily and leave. . . . A would-be "guiding" bird may sometimes follow a person for a very long distance (five miles is the maximum known to me) or for a very considerable period of time (half an hour is the maximum I know of) to attempt to get him to follow it.

Recent students of honeyguide behavior have reported somewhat different patterns, and these may well vary from place to place and from time to time. But there is no doubt that the birds exert considerable effort in attempts to attract the attention of people, that they do fly with frequent stops to the vicinity of bees' nests, and that if someone opens the nest they do eat honeycomb.

After describing this cooperative behavior in some detail Friedmann opens a section of his monograph (54–64) titled "Behavioristic level of the habit" as follows:

Use of the term "guiding," with respect to the behavior pattern that usually results in the follower arriving at a bees' nest, is unfortunate in that it implies a preexisting purpose or plan on the part of the bird, an intelligent activity far beyond the psychological capacity of any bird. . . . The word "guiding" has a purposive connotation which is applicable to the species but not to any of its members. . . . There are several features of "guiding" which further indicate its stereotyped nature. One is the fact that guiding is ordinarily not direct. The bird frequently leads in a most erratic course, often actually going a considerable distance beyond a bees' nest and then coming back to it. . . . If guiding were purposive in the individual this would be difficult indeed to explain, especially since there were no obstacles or barriers such as hills, ravines, etc to be bypassed. (54)

Friedmann illustrates several very indirect routes taken by honeyguides between the place where the leading began and the bees' nest where it ended, and he found he could cover the direct distance between these two points in half the time he had taken when following the bird. Yet, as pointed out by Isack and Reyer (1989), these birds did not move at random, and tended toward the location of the bees' nest, though their approach was indirect.

Friedmann advanced as another reason for concluding that the guiding is not intentional "the fact that on occasions the bird will lead not to a bees' nest but to a dead animal or to a live snake, leopard, rhinoceros, etc." One reason for this may be the numerous flies or other insects that are often present near animals such as those near which the honeyguide ceases its leading behavior. Friedmann also cites the following

episode as evidence that the honeyguides were not leading intentionally to a bees' nest whose location they knew beforehand:

Captain Davison . . . had a group of his natives at one of the rest camps in the Reserve when a honeyguide came to them and chattered and went through all the motions of trying to get them to follow it. Davison refused to let any of his boys go, but got them all on a truck and drove off to the next camp some five miles away. The bird followed them all the way and then Davison told one of the natives to get an axe and follow the bird. The honey-guide "led" this native to a bees' nest less than half a mile from the second camp, but which must have been at least 4½ miles from where the bird first began calling to them. (59)

Elsewhere in his 1955 monograph, and especially in later reviews of the same material, Friedmann claimed that these observations *prove* that the guiding behavior is carried out without conscious intention on the bird's part. For instance: "It is now known that this guiding behavior, which looks so purposive, is actually a form of excitement reaction on the part of the bird when meeting a potential foraging symbiont, and that the excitement dies down when the bird, with its symbiont near at hand, sees or hears swarming bees" (Friedmann and Kern 1956, 19). His 1955 monograph includes the statement: "The releasers of the instinctive behavior constituting 'guiding' are the sight or sounds of rats, baboons, and humans (away from villages). The stimulus which apparently brings these actions to a halt is the sight or sound of bees" (p. 59). And, later: "There is no occasion whatever to assume anything involving planning or intelligence on the bird's part. The behavior is wholly on an instinctive level, but it is something sought for by the bird, not merely something it does automatically when the necessary stimuli are present" (p. 163).

These statements are representative of the widespread efforts on the part of both psychologists and biologists to account for all animal behavior without allowing any role for conscious thinking or intentional planning. The observation that honeyguides do not go directly to a bees' nest is important and certainly argues against a detailed and accurate memory of the most direct route to the goal. But it scarcely proves the absence of any conscious intention. One obvious alternative would be an imperfect memory of where a bees' nest was located, even though the bird might recall that there was one in the vicinity. Or the bird might wait until it had enlisted a follower and then begin searching for a bees' nest. The available data are far from sufficient to confirm or disconfirm such hypotheses; but the important point is that scientists have been very quick to seize upon any failure of an animal to perform with perfect

efficiency and to offer such failure as evidence that it is a totally thoughtless robot.

In a truly revolutionary paper Isack and Reyer (1989) describe an intensive field study of the greater honeyguide in northern Kenya, extending over three years, in an area where honey from the nests of wild bees is an important part of the diet of the Boran people. This is dry bush country quite different from the forested areas where Friedmann had conducted most of his observations of the same species, but the guiding behavior was very similar to the displays and calls Friedmann had described. Some of the Boran people are professional specialists in honey gathering, and they rely on honeyguides to a considerable extent. Considering only days when they did find at least one bees' nest in an unfamiliar area Isack and Reyer (1989) report that "their search time per bees' nest was, on the average, 8.9 hours when not guided and 3.2 hours when guided." Very few of the bees' nests are located where the unaided birds can reach them, so that the guiding, and following, behavior is an effective form of behavioral symbiosis which has important benefits for both participants. The extensive observations of these birds by Short and Horne (1985) are quite consistent with the behavior described and analyzed by Isack and Reyer.

The Boran honey gatherers interviewed in their own language by Isack, who is himself a Boran, stated that the guiding behavior of the honeyguides "informs them about the direction of, the distance to, and their arrival at the colony [of bees]." Isack and Reyer tested this surprising statement by mapping several routes followed by honeyguides while guiding the professional honey gatherers. The results clearly confirmed that the starting direction was indeed almost always correct within 20 or 30 degrees, and the mean direction of all initial flight directions was within less than one degree of the bearing of the bees' nests to which they eventually led their human cooperators. As the bird travels toward the bees' nest, three properties of its guiding behavior decrease progressively: the distance between perches where it lands and waits for the man to catch up, the height of these perches above the ground, and the duration of periods when the bird flies off toward the bees' nest and then returns. This period varies between about half a minute and two minutes, and while it was not possible to follow the birds, it seems likely that they fly part or all of the way to their objective and then return to the man they are guiding.

The human honey gatherers communicate with the honeyguides. They use a loud whistle to attract the birds, and as they follow them "they whistle, bang on wood, and talk loudly to the bird to keep it in-

terested in the guiding.” When it has reached the vicinity of a bees’ nest the bird emits an “indication call” which is softer in tone than the calls during guiding, with longer intervals between successive notes.

Isack and Reyer observed the vicinity of bee nests from “camouflaged observation positions occupied before dawn,” and they saw honeyguides inspecting the nests, remaining only for about a minute before flying away. On cloudy and cool mornings when the bees were not aggressive, “the bird would fly straight into the entrance of the nest and peer into it.” Isack and Reyer could not gather data adequate to test two additional claims of the Boran honey gatherers: “(i) that a bird, flying lower than the treetops, will guide to a colony close to the ground, and (ii) that when nest distances become very long (about 2 km or more), the birds ‘deceive’ the gatherers about the real distance by stopping at shorter intervals. However, having found all the other Boran observations to be true, we see no reason to doubt the statements of these excellent ‘ethologists.’”

These recent discoveries by Isack and Reyer are most revealing, and show that Friedmann’s interpretations, reached in the heyday of behaviorism, clearly failed to do justice to the versatility of which the honeyguides are capable. The close correlation of the birds’ initial directions of flight and the straightness of the routes along which the honey gatherers are led, demonstrate clearly that the birds knew the location of the nest to which they were leading their cooperators. Whether the variations in perch height and length of flights between perching are intended to inform the follower is more difficult to ascertain. But even if they are not, they provide evidence that the bird is paying attention to its memory of the nest location. Behaviorists can translate these observations into a series of stimulus-response contingencies, but the resulting positivistic account becomes more and more unwieldy as more is learned about the details of the birds’ actual behavior. To assume a simple conscious intent to lead the follower to the bees’ nest and get food after he has opened it seems a more parsimonious and reasonable interpretation.

### A Parrot Who Means What He Says

“Parroting” has become a term for imitation of speech without understanding what it means. African gray parrots (*Psittacus erithacus*) are especially proficient at mimicking human speech, but other parrots, mynah birds, starlings, and other species can also mimic words well enough that they can easily be recognized by human listeners. The effec-

tiveness with which parrots and other mimetic birds can imitate a wide variety of words, as well as other sounds, has led their owners to teach them whatever comes to mind. The results are often entertaining; but the meanings of the words imitated are mostly so remote from anything a bird could possibly comprehend as to reinforce the widespread conviction that avian mimicry entails no understanding whatever. If it has not already been done, an African gray parrot could undoubtedly be trained to say "Read my lips!" just as one trained by Stevens (1888) learned to say "Hurrah for Blaine and Logan" during the campaign of 1884.

Yet some words that parrots learn do have a simple and direct relevance to their situation, as when they learn to ask by name for particular foods. Although this is grudgingly recognized, a sort of simplicity filter has tended strongly to rule out of scientific thinking the notion that a bird might understand that a simple meaning is conveyed by a sound it has learned to imitate. This type of simplicity filter was made to seem more plausible by the failure of several efforts to train parrots to emit particular sounds in order to obtain a food reward. The most often cited examples of such efforts are those of Mowrer (1950, 1960a, 1960b, 1980) and Grosslight and Zaynor (1967).

It is perhaps no accident that in the 1950s when behavioristic learning theory was dominant in psychology it was O. H. Mowrer who became interested in "talking" birds. For he was sufficiently uninhibited by behaviorism to write: "If . . . we sometimes speak of 'consciousness' (a tabued word for the behaviorists), this is not just a friendly gesture to the past or concession to common sense; it represents instead the growing conviction that the objective study of behavior has now reached the point where some such concept is essential . . . if consciousness were not itself experienced, we would have to invent some such equivalent construct to take its place" (Mowrer 1960, 7).

Mowrer later (1980) describes how he "acquired a collection of parrots, mynah birds, parakeets, magpies and crows, and set about learning how to teach them to 'talk.'" It is not clear from his publications to what extent he actually tried to elicit vocalization by means of operant conditioning with food as a reward, but his efforts were apparently unsuccessful. For he continues:

The only systematic and extensive investigation of this problem thus far reported, in so far as I am aware, is that of Grosslight and Zaynor (1967). The mynah birds which were used as experimental subjects were put into sound-

proof boxes, and there periodically heard a tape-recorded word or phrase which was then followed by a pellet of food. . . . These subjects should have learned to reproduce the "conditioned stimulus" (word), that is, to imitate. They did not. . . . Perhaps we get a clue from the fact that there were two or three mynahs around Grosslight's laboratory which his assistants had converted into "pets," and they were all fluent talkers. (1980, 51-54)

It is characteristic of the behavioristic *Zeitgeist* of the mid-twentieth century that Mowrer's work has since been cited primarily as evidence that because birds cannot be trained to imitate speech by means of standard operant conditioning methods, their imitation cannot entail any understanding of the meanings conveyed by the words they mimic. This was clearly not what either Mowrer or Grosslight and Zaynor concluded. Instead they recognized that interactive exchanges of sounds with companions was probably a necessary condition for the development of "talking" in birds. Ethologists proceeded to study the use of complex vocalizations by parrots, Indian Hill mynahs and other birds under natural conditions and found that imitation of companions plays a large role in their social behavior. Young birds pass through a stage when they emit varied and imperfect versions of the sounds they will use as adults, and they seem to enjoy repeating and imitating sounds they hear around them. The social context, and the responses of other birds are important factors in song learning, as demonstrated for example by West and King (1988) with cowbirds. Females of this species respond to a small subset of male songs with a rapid wing flick, and this is apparently recognized by the males as a sign of readiness for copulation.

An important advance was made by Todt (1975), who developed an effective training procedure called the model/rival approach. His procedure was much closer to the natural social exchanges by which birds learn their vocalizations, although with human companions rather than other birds. He exposed a mimetic bird such as the African gray parrot to a cooperative human trainer who talked in the bird's presence to another person acting as a rival, in effect competing with the parrot for the trainer's attention. Irene Pepperberg (1981) improved this procedure by having two trainers talk about objects in which their parrot seemed interested, one asking for one of these objects, the other giving it to her or withholding it according to the correctness of her verbal requests. The trainers exchanged roles from time to time. Using this method she succeeded in training a male African gray parrot named Alex to use imitations of several English words in an appropriate fashion. In his first

26 months of training Alex acquired a vocabulary of nine names, three color adjectives, two phrases indicating simple shapes, and he came to use “no” in situations where he was distressed and seemed unwilling to do what his trainers wanted, or when rejecting something offered to him.

Alex has subsequently learned numerous uses of his imitated English words. When shown familiar objects and asked “What color?” or “What shape?” Alex learned to answer correctly more than 80 percent of the time, which is far better than chance because he had to select one of five colors or four shapes (Pepperberg 1987b). In further experiments he learned to say the numbers 2 to 6 plus the name of the objects when presented with sets of two to six familiar things. His overall accuracy in these tests was 78.9 percent correct, but more than half of his errors were responses in which he named the objects correctly but omitted the number. In such cases the further query “How many?” produced the correct response 95 percent of the time (Pepperberg 1987a).

In other experiments Alex was shown two objects (which might be either familiar or things he had never seen before) and required to say what was the same or different about them (Pepperberg 1987b, 1988, 1991). They differed in color, shape, or material, and Alex usually gave the correct response—“color,” “shape,” or “matter” (which he pronounced “mah-mah”)—to designate the material of which the object consisted (paper, wood, cork, or rawhide). His responses to “What’s same?” or “What’s different?” were 82–85 percent correct when there were three options—color, shape, or material—so that a chance score would be only 33 percent correct. In further tests of this general type, some pairs were identical, while others were totally different. In the former case Alex learned to respond to the question “What’s different?” by saying “None.” When the test objects were very different and Alex was asked “What’s same?” he would also answer “None.” His accuracy in these tasks was about 90 percent.

In still more recent experiments Alex is shown any collection of objects and asked any of the following four questions: “What color is X?” “What shape is X?” “What object is Y?” or “What object is shape Z?” where X might be the name of any of several familiar objects, Y might be any of seven colors, and Z any of five shapes. He had learned all these words and used them correctly in previous experiments. His accuracy in responding was about 81 percent. These questions were mixed with other tests, so that each one was presented only at long intervals. To answer correctly Alex had to understand all the words in the question

and use this understanding to select the correct reply from his vocabulary (Pepperberg 1990, 1991).

These findings constitute a truly revolutionary advance in our understanding of animal mentality, comparable to von Frisch's discovery that honeybees use symbolic gestures to communicate direction and distance to their sisters, as discussed below. Because they are such startling extensions of what we had previously believed possible for any bird, it is very important to consider carefully whether there might be some flaw in these experiments. In short, can we really believe that a parrot can make such judgments and express them by using words he has learned to imitate?

It is unfortunate that Pepperberg's pioneering work is based on the behavior of a single bird. To date no one else has apparently attempted to replicate Pepperberg's experiments, but she has begun to extend her experiments to include another parrot. Both steps are highly desirable; but pending such essential replication we can inquire as critically as possible what flaws might have escaped our notice. The first thought of any student of animal behavior is that some sort of inadvertent cuing may have taken place, that Alex responded not to the actual properties of the objects he was shown but to some unrecognized behavior of the trainer who presented the objects and asked the questions, something analogous to the cuing that explained the apparent ability of Clever Hans to perform feats of mental arithmetic. Such inadvertent signals would have to be quite subtle, some gesture that Alex took to mean he should say "same," "blue," "wood," "none," or any of the several other words he had learned.

Alex was initially quite sensitive to the presence of his familiar trainers. He acted frightened in the presence of strangers, so that to assure his attention and cooperation his principal trainer, Pepperberg, had to be present during critical testing of his discriminatory responses. During all tests, as opposed to training sessions, Pepperberg, who is keenly aware of the dangers of inadvertent cuing, sat in one corner of the room, did not look at Alex, and did not know what was presented to him by a so-called secondary trainer. The latter was familiar to Alex but had not been present when he was trained in the task under investigation. In other words, this secondary trainer was not present when a primary trainer had presented the test objects and trained Alex to say "same," "different," "none" or whatever was the correct response. Thus Alex had no opportunity to learn any inadvertent cues that might accompany the presentation of various objects or combinations by the secondary



trainer. If he was responding to some unrecognized cue specifying which of numerous words in his vocabulary he should utter on a given occasion, it must have been one that any person would exhibit when showing Alex various objects. This seems highly unlikely, to say the least. More recently Alex has demonstrated that he can answer correctly about 80 percent of questions asked by relative strangers when Pepperberg is not present.

Therefore it seems reasonable to conclude that a parrot can learn both to understand and to communicate about several simple properties of familiar objects (color, shape, material) as well as such basic relationships as same or different. Pepperberg makes no claim that Alex has learned anything approaching the versatility or complexity of human language; but he does seem to have demonstrated some of the basic capabilities that underlie it. More important is the strong indication that Alex thinks about colors, shapes, sameness, and so forth. To be sure, those inclined toward a sleepwalker view of nonhuman animals may insist that he is an unconscious robot so contrived that he gives the correct verbal responses. But this insistence must be based on other considerations than his ability to use words meaningfully. In short, he gives every evidence of meaning what he says.

## *Symbolic Communication*

**E**xploiting newly discovered sources of food is a very common problem for animals that live in cooperating groups. To consider a simple example involving the smallest possible group, when insectivorous birds are feeding a nestful of young, they need to locate and capture quite large numbers of insects. They are not alone in this search; other birds and other insectivorous animals are also busy hunting, and the insects themselves are not exactly cooperative in making themselves available. When both parents are feeding nestlings, one parent sometimes finds an aggregation of edible insects at some distance from the nest when the other is less successful. In this situation it would clearly be advantageous for the former to convey to its mate the location of this newly discovered source of food. We do not know whether this happens or not. It has not been observed, but the types of observation that would be necessary to reveal it are difficult and have not been seriously undertaken, to the best of my knowledge. One would have to follow both foraging parents, note when one of them was having better success than the other, see whether they interacted back at the nest, and, if so, whether the less successful parent then flew to the food source discovered by its mate.

This would be a special case of an “information center” where animals may learn from their companions where to locate food, as suggested by Ward and Zahavi (1973). Many recent studies (for example Richner and Marclay 1991) have failed to support the hypothesis that animals learn in this way about the location of food. Perhaps as ethologists begin to devote more attention to animal cognition and intentional communication, the necessary studies will be carried out and will reveal whether or not this sort of efficient communication about newly discovered food sources does occur in birds.

Other social animals certainly do share information about newly discovered food sources, as reviewed by Hölldobler and Wilson (1990).

One of the best examples involves the weaver ants, whose ingenious cooperative construction of leaf nests was described in chapter 4. Gathering the food needed by any large colony of ants requires a great deal of effort on the part of many of the nonreproductive workers. They often search a relatively wide area and after they have found food return to the nest and recruit many of their sisters to join them in gathering this food. Most species of ants lay odor trails along the route from the food source back to the nest. But this in itself may not be enough, because workers that have not been to the food must be induced to follow the odor trails. Chemical signals are transferred from returning foragers to other members of the colony as they feel each other with their antennae. The forager often regurgitates food from her stomach which others take up in a behavior pattern known as trophallaxis.

In some ants the returning forager moves her body rapidly from side to side while engaging in mutual palpation and trophallaxis with one of her sisters. In *Camponotus serviceus* this behavior induces the recruited ant to grasp the abdomen of the forager, and the latter then moves out along the odor trail she laid down on her return to the colony (Hölldobler 1974, 1977). This results in tandem running out to the food source. Another very important form of recruitment occurs when the colony is threatened by aggressive or competing members of other colonies or other species. The weaver ants show a significant difference in their recruiting behavior according to whether recruitment is for food gathering or fighting off intruders.

Hölldobler and Wilson (1978) have studied in detail the behavior of weaver ant workers after they have returned to the colony either from food sources or from encounters with intruders. The intruders may be members of another colony of the same species that are more numerous and aggressive, or they may be other insects. The recruiting weaver ant engages in a series of face-to-face encounters with nestmates at or close to the leaf nests. The recruiter makes lateral movements of her head, which often induce the other ant to follow the odor trail she has just laid down. These recruiting gestures differ according to what it is the recruiter has returned from. The principal difference is that when recruiting to food sources, they move the head in lateral wagging motions. But when they are returning from an encounter with intruders, they recruit other workers by jerking their bodies back and forth toward and away from the nestmate rather than from side to side. Hölldobler and Wilson also describe other communicative gestures used when stimulating nestmates to move to another location, but the distinction between gestures for recruiting to food and for combating intruders is

especially clear-cut. The gestures used in recruiting for fighting resemble in some ways the movements employed in actual combat. This may be a ritualized imitation of actual fighting, a sort of intentional pantomime. Whether intentional or not, this differential recruitment is effective, and numerous workers are induced to move rapidly out either to gather the recently discovered food or to fight the intruders.

Why are different gestures used for these two purposes? If the only function of the communication were to recruit nestmates, it would seem unnecessary to use a different gesture in the two situations. Perhaps the recruited ants are better prepared for either food gathering or fighting if informed which to expect as they move out from the nest. These recruiting gestures are undoubtedly accompanied by the transmission of odors and chemical signals, and for all we know these may also provide information about what is located at the end of the odor trail.

Another feature of weaver ant recruitment also suggests thinking about the need to recruit nestmates. Some of the ants receiving the recruiting gestures do not follow the odor trail but turn to other workers and repeat the recruiting gestures even though they have not been directly stimulated by intruders or newly discovered food. This sort of chain communication whereby one original recruiter indirectly stimulates large numbers of nestmates is almost unique in animal communication. If we allow ourselves to postulate, tentatively, that these ants might be thinking in simple terms about such important matters as gathering food or fighting intruders, these somewhat specialized gestures may be interpreted as evidence of what they are thinking about. The practice of chain communication is especially significant, because the ant that has been stimulated by recruiting gestures and then repeats these gestures may be expressing a simple thought that has been conveyed to her through the communicative process itself rather than by some external stimulation.

These two kinds of recruiting gestures are an extremely limited form of somewhat symbolic communication. The similarity remarked upon by Hölldobler and Wilson between the gestures used to recruit for fighting and the actual motions of fighting suggests that the communication is iconic rather than symbolic. In this usage iconic means that the signal resembles the action or thing that it represents. Thus making a sound characteristic of a particular sort of animal as a symbol to represent that animal, such as "bow-wow" for dogs, is iconic, whereas the word "dog," which has no particular resemblance to the animal in question, is not. On the other hand, the recruiting gestures for food sources

do not seem to be iconic. It will be of great interest to learn more about these processes of communication when they can be studied with attention to their possible significance as indications of the thinking of the communicating animals.

Humphrey (1980) has extended an earlier suggestion by Jolly (1966) that consciousness arose in primate evolution when societies developed to the stage where it became crucially important for each member of the group to understand the feelings, intentions, and thoughts of others. When animals live in complex social groupings, where each one is critically dependent on cooperative interactions with others, they need to be "natural psychologists," as Humphrey puts it. They need to have internal models of the behavior of their companions, to feel with them, and thus to think consciously about what the other one must be thinking or feeling. Following this line of thought, we might distinguish between animals' interactions with some feature of the physical environment or with plants, on the one hand, and interactions with other reacting animals, usually their own species, but also with predators and prey, as discussed in chapter 3. While Humphrey restricted his criterion of consciousness to our own ancestors within the past few million years, it could apply with equal or even greater force to other animals that live in mutually interdependent social groups.

### The Symbolic Dances of Honeybees

The most significant example of versatile communication known in any animals other than our own species is the so-called "dance language" of honeybees. This type of communicative behavior is so strikingly different from all other known kinds of animal communication that it has been difficult for inclusive behaviorists to integrate it into their general understanding of animal behavior. The difficulty is exemplified by the behavioral ecologist Krebs (1977), who called these dances an "evolutionary freak." The versatility of honeybee learning has been reviewed by Gould and Towner (1988); and many of the complex effects of overlearning and extinction studied by psychologists in rats and pigeons have also been found in honeybees, for example by Bitterman (1988), Shinoda and Bitterman (1987), Couvillon, Leito, and Bitterman (1991) and Lee and Bitterman (1991).

Beekeepers and students of bee behavior had noticed for centuries that worker honeybees sometimes move about over the surface of the honeycomb in agitated patterns called dances. It was also well known that once a single foraging worker has discovered a rich source of food,

such as flowers that have just come into bloom, many other bees from the same colony may arrive a few minutes later, so rapidly that they could not all have found the food by individual searching. This suggested that some sort of recruiting communication occurred, but how this was achieved remained almost totally unknown until the work of Karl von Frisch, whose work has been mentioned several times in earlier chapters. He was a brilliant Austrian zoologist who carried out most of his research at the University of Munich, beginning about 1910. Quite early in his career he proved by elegant simple experiments that bees were capable of discriminating hues. He was led to this discovery by the simple naturalist's belief that the striking colors of flowers must be perceptible to the insects that visit them to obtain nectar and pollen. Early in the twentieth century, prevailing scientific opinion was strongly negative about color vision in invertebrates. But von Frisch developed simple and ingenious experiments demonstrating conclusively that honeybees have excellent color vision.

In the 1920s, when studying the sensory capabilities of honeybees, von Frisch noticed that the agitated dances were carried out by workers that had visited sources of food. In order to see what bees did on returning to the hive, he constructed specialized beehives with glass windows that allowed a clear view of their behavior as they crawled over the honeycomb. To study foraging behavior he set out dishes containing concentrated sugar solutions, which bees visit and take up eagerly just as they take nectar from flowers. To identify individual bees he marked them with small daubs of paint on the dorsal surface while they were sucking up sugar solution. The bees he had marked at his dishes of sugar solution danced in circles, alternating clockwise and counterclockwise motions. At the same time he noticed that others returning with loads of pollen were carrying out a very different type of dance. He could tell that they had gathered pollen because honeybees carry substantial amounts of pollen grains packed between hairs on their legs. These pollen gatherers performed what are called *Schwanzeltanzen* in German, customarily translated as waggle dances. In a waggle dance the bee walks rapidly in a straight line while moving her abdomen back and forth laterally at about thirteen or fourteen times per second. Then at the end of this straight wagging run she circles back and repeats the straight part of the dance, followed by alternating clockwise and counterclockwise returns to the starting point of a series of straight wagging runs. Although the bee may move a short distance between successive cycles of the waggle dance, the basic pattern is relatively constant under given conditions. Von Frisch thus concluded that the two types of dance were

somehow related to the sort of food being brought back to the colony, a reasonable interpretation of the observations he was able to make at the time.

Only much later, during World War II, when his laboratory in Munich had been seriously damaged and he was studying bees at his country estate in the Austrian Tyrol, did he have occasion to move the artificial feeding dishes to a considerable distance from the observation hive. When he did this he discovered that the bees gathering sugar solution from more than about one hundred meters performed waggle dances rather than the round dances he had always associated with sugar gathering (von Frisch 1950, 67–72; 1967, 57–235). This had escaped his notice previously, because for reasons of simple convenience he had set out his dishes of sugar solution relatively close to the observation hive so that he or his assistants could remain in touch while marking bees at the feeder or observing them in the hive.

It is very important to appreciate that these dances occur only under rather special conditions. They are part of an elaborate nexus of social communication that goes on almost continuously in a beehive, as described by Lindauer (1971) and Seeley (1985, 1986, 1989a, 1989b). The workers move about a great deal and interact with their sisters by feeling them with their antennae and being felt in return. There is a sort of mutual palpation in which the two bees face each other and feel each other's antennae and head region. At this time one of the bees often regurgitates a small portion of her stomach contents, which is taken up by the other. This is very similar to the trophallaxis of weaver ants and other social insects. It is very widespread among social insects and serves to convey not only food material but also the odors that accompany it. In colonies of specialized social insects such as honeybees the queen, the larvae, and younger workers obtain their food in this way. Trophallaxis is so widespread that a given molecule of sugar ordinarily passes through several stomachs before it is finally regurgitated into one of the cells in the honeycomb. By this time the original nectar gathered from the flowers has been modified into honey. Pollen grains transported in specialized pollen baskets formed from stiff hairs on the legs are also transferred to other workers before being stored. During round and waggle dances other bees cluster around the dancer and follow her movements. From time to time they make a brief sound that seems to cause the dancer to stop and engage in trophallaxis with one or more of her sisters.

In spite of all this activity, worker honeybees seem to be doing nothing at all much of the time, but it is difficult to determine by simply

watching them whether their leisurely moving about the hive is idle loafing or whether they are sampling odors and other conditions in ways that will later affect their behavior. The workers often take food from partially filled cells, into which other workers are still adding honey or pollen. Thus the food stores of a beehive are in a constant state of flux, with new material being added after foragers have brought it back, but also constantly being drained by workers, which obtain much of their food in this way.

When a forager returns to the hive with a stomach full of nectar, she ordinarily finds other workers ready, after a brief period of mutual palpation, to take her stomach load by trophallaxis. These other workers then store the somewhat modified nectar in partly filled cells, or they may transfer it to third parties before it is finally stored. This widespread process of mutual palpation and trophallaxis serves also as a sort of communication, because the ease or difficulty with which a returning forager can transfer her load provides information about the general situation in the colony. This is particularly important when conditions are not optimal and when something is in short supply. The most common shortage is of carbohydrate food. The workers are informed of this by the relative emptiness of storage cells, and when conditions are truly severe, capped cells may be opened and the honey consumed. This results in an eagerness to receive regurgitated nectar during trophallaxis with returning foragers. When, on the other hand, honey is abundant but pollen is in short supply, foragers returning with stomachs full of nectar have more difficulty finding a sister to whom they can transfer their load. Whether there is some chemical or other signal that conveys more than a reluctance to receive one type of material is not clear. But somehow foragers are induced to change what they seek outside the hive.

This distinction becomes all the more clear under special conditions of overheating. When the hive temperature rises above approximately 35 degrees C, workers returning with either sugar or pollen have difficulty unloading. But workers that have gathered water regurgitate it in small droplets, and other workers fan vigorously with their wings, producing a circulation of air that cools the hive by evaporation. Under these conditions foragers shift from gathering nectar or pollen and visit places where they can take up water. It is not clear just how this transfer occurs, whether the high temperature directly stimulates the returning forager, along with her difficulty in unloading whatever she was bringing in previously, or whether some sort of information is transferred from other workers.



The important point is that the older workers that fly outside the hive searching for things needed by the colony shift their searching behavior between different commodities according to the needs of the colony. This network of social communication conveys to the older workers not only what is required by the colony but how badly it is needed. Thus when a forager leaves the hive, she has been induced to search for some particular thing, and this motivation clearly varies in intensity. The most common need is for carbohydrate food, so that the nectar of flowers is the usual target of this searching activity. But sometimes it may be pollen grains or water. Under other special conditions the need may be for waxy materials used in building honeycomb. This need is relatively rare in agricultural beekeeping practice because beehives have been built to provide a waxy foundation, but under natural conditions honeybees and other bees must build their own wax foundation or plug holes in a natural cavity. Dances do not occur at all when everything is going nicely and nothing is in short supply. Foragers return with nectar or pollen, these substances are transferred to other workers, and the net stores of both carbohydrate and protein food are either constant or slowly increasing. Under these favorable conditions it seems that workers can find adequate supplies of nectar and pollen by individual searching efforts.

Under the special conditions when something has been in short supply, older workers ready to fly outside the hive somehow receive the message that sugar, or something else, is very badly needed. When they have discovered a rich source of nectar they return to the hive and engage in communicative dances. After walking a short distance in from the entrance of the hive, and usually after antennal contact with other workers, the returning forager begins either round dances or waggle dances. Dancing is not something the bees do mechanically and automatically, but only as part of the larger social nexus of communication. This point is often overlooked in elementary discussions of the bee dances. The dances are entirely dependent on the presence of an audience of other bees.

With this background we can better appreciate the symbolic nature of the honeybee communication system. It is partly a chemical communication system, for the odors of flowers are conveyed along with the nectar or pollen. And when bees visit desirable things, they often mark their location with secretions from certain glands that produce a long-lasting odor which serves to attract searching foragers. But in addition to these specific odors that are transmitted, the dances convey the direction and distance to the food by a sort of geometrical symbolism.

Round dances are performed when food has been discovered relatively close to the hive, and waggle dances are used for desirable things located at a greater distance. The transition from round to waggle dances is gradual, and it occurs at different distances ranging from two or three meters in the Indian species *Apis dorsata* and *A. florea* to 50–100 meters in the widely used Carniolan strain of European honeybees. In a typical round dance a bee circles alternately clockwise and counterclockwise, although occasionally two cycles may be executed in the same direction. When von Frisch originally discovered that round dances were used for food sources at relatively short distances and waggle dances for those farther from the hive, he concluded that the round dances contained no directional information and simply informed recruited workers to search in all directions close to the hive. He also found that bees stimulated by round dances arrived in approximately equal numbers at experimental feeders located in different directions within a few meters of the hive. Many interested scientists have observed and made motion pictures of round and waggle dances over a forty-year period, but only recently has it been noticed that even at very short distances the point at which the circling reverses does contain directional information of the same kind conveyed by the waggle dances discussed below (Kirchner, Lindauer, and Michelsen 1988). The fact that it took so long to appreciate this simple fact indicates how easily we overlook matters that do not readily fall into our preconceived patterns of expectation.

The transition from round to waggle dances begins by a very brief lateral vibration of the bee's body just at the moment when she has completed one circle and is about to begin circling in the opposite direction. As the distance to the food increases this lateral wagging motion lasts longer and the bee walks in a straight line for a gradually increasing distance. This can be observed with the same bees by inducing them to gather concentrated sugar solution from an artificial feeder which is gradually moved away from the hive. This experimental procedure is effective only when the colony is seriously in need of additional sugar. When the distance is gradually increased, beginning at a very few meters from the hive, it is possible to see the gradual transition from an almost instantaneous lateral vibration at the moment when the round dance is reversed in direction to an increasingly long straight wagging run. At distances of a kilometer or more the wagging run is ten or eleven millimeters in length.

The most significant of von Frisch's discoveries was that the direction of the straight wagging run was correlated with the direction that the

dancer had flown from the hive to the source of food. This insight was possible only when he was able to observe waggle dances performed by bees that had returned from known food sources lying at considerable distances in various directions. Ordinarily this is not possible, because honeybees are too small and fly too far and too fast to permit direct observation. In his early experiments, von Frisch saw no reason to move his artificial food sources more than a few meters from the hive. In the 1920s it would have required a truly superhuman level of enterprising imagination to suggest that an insect might indicate the direction to a food source by some form of communicative behavior. Even a brilliant scientist who had already challenged some of the established “nothing but” dogmas of his time did not make the leap of inference necessary to imagine that the waggle dances which he and many others had observed could conceivably serve to communicate direction toward a source of food. This leads one to wonder what other versatile ingenuities of animals might be staring us in the face but waiting to be correctly interpreted.

The specific correlation between direction of the wagging run and direction toward the food takes the following form: When the food is in the direction of the sun, outside the hive, the waggle dances are oriented straight up on the vertical surface of the honeycomb. If the food is located in the opposite direction from the sun, the dances point straight down, and under other conditions the angle between the direction to the food and the azimuth bearing of the sun corresponds to the orientation of the wagging run relative to straight up. If the food is 90 degrees to the right of the sun, the dances are 90 degrees to the right of vertical.

This relationship between a direction taken by a flying bee outside the hive relative to the sun and the direction of its communicative wagging run inside the pitch dark hive is more truly symbolic than any other known communication by nonhuman animals. But one should not take this correlation to mean that the directional communication is perfectly precise. At gradually increasing distances, as the bees change from round dances to waggle dances, the straight runs do not at first point directly in the appropriate direction. Instead they alternate between being several degrees to the right or to the left of the correct distance according to the rule stated above. As the distance increases this deviation diminishes, so that by several hundred meters each waggle run points in almost exactly the same direction. The accuracy of information transfer has been measured by Towne and Gould (1988) by setting out test feeders in a variety of directions and distances with careful control

for the complicating effects of odors. The majority of the recruited bees came to feeders within about plus or minus 15–20 degrees and plus or minus about 10–15 percent of the distance indicated by the dances.

Thus the system is far from perfect, but the waggle dances communicate three types of information that are all important to the bees. These are (1) the direction toward the food, expressed relative to the position of the sun, (2) the distance to the food which is correlated with the duration and perhaps length of the wagging run, and (3) the vigor of the dances which conveys the desirability of whatever the bee is dancing about. The detailed nature of distance communication has been difficult to determine. The number of wagging movements is correlated with the distance a bee must fly. But since the rate of wagging and the rate of forward movement are quite constant, both the length of the wagging run and its duration are also closely correlated with distance. While statistical analysis suggest that the duration is a better indication of distance, it is not possible from currently available data to be certain which property of the wagging run is actually perceived by other bees and used to determine the distance they will fly.

The vigor or intensity of waggle dances is easily recognized by experienced observers, for some dances seem clearly more energetic than others, and these ordinarily result when foragers have found a rich source of sugar solution or something else that is important to the bees. The concentration of sugar in an artificial feeder can be more easily manipulated by experimenters, so that it has been studied more thoroughly. But it is clear that under relatively constant conditions when carbohydrate food is scarce and dancing is actively under way, the dances are much more intense when the foragers have visited sugar solutions with a high concentration. One difference is that dances from rich sources are continued for a long time while dances from less concentrated sugar solutions may be continued only for a few cycles and then broken off, as discussed by Seeley and Towne (in press).

Another important point about the waggle dances is that they serve to convey information to other bees inside the totally dark beehive when the subject of the communication is something entirely different from the immediate situation, namely the direction a bee should fly out in the open air. Thus the communication has the property of displacement; the bees communicate about something displaced in both time and space from the immediate situation where the communication takes place.

Wenner (1959, 1962b), and Esch (1961, 1964) discovered that faint sounds accompanied the waggle dances. These are not ordinarily loud

enough to hear through the glass window of an observation hive and require that the glass be removed so that the dances can be observed directly. This is obviously somewhat hazardous, since several hundred bees are completely free to fly out. But if the glass is gently removed most of the bees stay in the honeycomb, and many detailed experiments have been carried out with observation hives that can be opened. Ordinarily this is done with a darkened room around the hive, but even this is not entirely necessary, and quite bright lights can be used for photography or video recording, provided that the bees are not disturbed excessively. The sounds accompanying waggle dances are brief pulses with a fundamental frequency of about 250–280 Hz; each lasts only for a few waves but the pulses are repeated as a sort of interrupted buzzing. The fundamental frequency is nearly the same as the wingbeat frequency when the bees are flying, but the wings move only a fraction of a millimeter. The sounds and wagging movements are not always synchronous; in long-duration dances reporting highly desirable food, the sound may be delayed by a substantial fraction of a second (Griffin and Taft, in press).

Esch (1963) concluded the desirability of food or other commodities seems to be conveyed, at least in part, by the intensity or temporal pattern of these dance sounds, which seem to vary with the desirability of the food being gathered. But Wenner, Wells, and Rohlf (1967) did not find such variations, and it remains unclear whether the dance sounds convey information about food quality. One possibility is that the temporal relations between wagging movements and sound emission might convey this or other types of information. Further evidence of their importance has recently been provided by Towne (1985), who studied two closely related species of bees in India, *Apis dorsata* and *A. florea*, which use waggle dances but nest in places where light is available. They make no dance sounds, although in other aspects of their dance communication they are similar to European *Apis mellifera*. It seems clear that only honeybees and their close relatives that dance inside dark cavities make sounds during their waggle dances.

Interpretation of these observations was initially difficult because honeybees appeared to be deaf. Despite several attempts to do so, no one had been able to demonstrate any responses to airborne sounds. This suggested that the sounds heard by human observers might be an incidental by product of a mechanical signal that was transmitted either by vibratory motions of the surface on which the bees were standing or in some other manner. This situation has been considerably clarified through quantitative acoustical experiments by Michelsen and his col-

leagues (Michelsen, Kirchner, and Lindauer 1986; Michelsen, Kirchner, Andersen, and Lindauer 1986; and Michelsen, Towne, Kirchner, and Kryger 1987). The most important point clarified by these recent experiments is that the changes in air pressure which we detect as sounds, either by hearing them directly or via microphones, are only one physical aspect of the signals generated by dancing bees.

When any solid object oscillates against the air, whether it be a dancing bee or a loudspeaker diaphragm, air in the immediate vicinity moves back and forth at the frequency of the movement. Close to the vibrating object this motion of the air is the primary physical process, but magnitude of air movement falls off with distance very rapidly. The oscillating movements of the air also generate traveling sound waves which are areas of very slight compression and rarefaction that spread outward at the speed of sound (approximately 344 meters per second in air). It is of course qualitatively true that in order to produce a region of higher pressure some air molecules must move into such a region, but the amount of air that moves back and forth in a traveling sound wave is very small compared to that which moves about close to the vibrating source. This difference leads to the physical distinction between near field and far field sounds. In the near field the air motion is large and in the far field it is very small, because its magnitude falls off rapidly with distance from the source.

The bees that are stimulated by a dancer are ordinarily within less than one body length, and this is definitely in the near field. The sounds with which we are most familiar are far field pressure waves. Bees and most insects lack specialized auditory receptors for sound pressures, although a few specialized insects such as some of the moths that respond to the orientation sounds of bats do have sense organs adapted for responding to sound pressure. What bees and many other insects have instead are very sensitive hair-like sense organs that respond well even to feeble air movements, whether these be unidirectional or oscillating at frequencies of a few hundred Hz. Thus it is not surprising that honeybees do not respond to far field sounds, but such insensitivity tells us nothing about their sensitivity to near field acoustic stimulation which consists primarily of oscillatory air movements.

Michelsen, Towne, Kirchner, and Kryger (1987) measured the near field component of the dance sounds and found these to be quite intense, provided the measuring devices were within a few millimeters of the dancer. In further experiments Towne and Kirchner (1989) and Kirchner, Dreller, and Towne (1991) found that honeybees respond to the near field, air movement component of sound similar to the dance

sounds. Using sound sources that generated either primarily near or far field sounds of either 265 Hz or 14 Hz, they were able to show clear responses to the near field signals but not to the far field sound pressure stimulation. The latter had been used in previous attempts to learn whether bees could hear.

The situation is further complicated by the fact that honeybees also transmit acoustic signals as vibrations of the substrate. With appropriate vibration detecting sensors Michelsen, Kirchner, Andersen, and Lindauer (1986) showed that the dance sounds are transmitted only very feebly into the honeycomb. But another sound at about 320 Hz is emitted by bees following a dancer; this is believed to serve as a request for the dancer to stop and regurgitate food samples. These sounds are transmitted through the substrate. When the honeycomb was set into vibration by artificial devices at this frequency dancing bees stopped dancing as they do when this so-called begging signal is generated by other bees clustered around a dancer.

Another quite different type of acoustical signaling is carried out by honeybee queens. When larvae have been fed appropriately by workers they develop into queens, and often several queens are present in separate cells. At this time, it has long been known that the queens emit two kinds of sounds called tooting and quacking. These are transmitted through the honeycomb substrate and are sensed by other queens. The tooting is produced by a queen who has emerged from her cell and the quacking signals come from queens still confined within cells. Usually the original queen together with a very large number of worker bees departs from the hive and forms a new colony. One of the new queens then cuts a hole in the side of the other queen cells and kills the occupants. Thus this exchange of acoustical signals is an important part of the social behavior of a honeybee colony around the time of swarming.

Michelsen, Kirchner, and Lindauer (1989) have succeeded in constructing a model honeybee that can transmit signals which direct recruits to search for food in particular directions. This exciting development is still at a very early stage, and all that can be said is that in a general sense the model does work. The reason it has worked better than previous attempts is probably that the near field acoustical signals have been reproduced more accurately. It will be of great interest to follow future developments in this new technology for studying the symbolic dance communication of honeybees.

It has been so astonishing to find insects communicating in such a versatile and symbolic fashion that some skeptics have remained uncon-

vinced that the system really functions as von Frisch described it (Rosin 1978, 1980, 1984, 1988; Wenner 1989; Wenner and Wells 1990). Both Rosin and Wenner consider von Frisch's discoveries suspect because they imply, for Wenner (1989, 119), that bees are "capable of human-like communication (language)," or because, according to Rosin (1978, 589) "a hypothesis which claims a human-level 'language' for an insect upsets the very foundation of behavior, and biology in general." These critics, and doubtless others, are so certain that symbolic communication is a unique human capability that they go to great lengths to deny the significance of the many experiments demonstrating that the dances convey information about distance, direction, and desirability. They do not deny that the pattern of the dances is correlated with the location of a food source, but claim that recruited bees simply search for the odor they have learned from the dancer is associated with the food. In some ingenious experiments by Gould (reviewed by Griffin 1981), bees were induced to point their dances in a direction different from the actual direction from which they had returned. Test feeders were set up in the form of traps that allowed counting of the number of recruits arriving at different places, but prevented them from leaving and possibly introducing complications. The results were that most of the recruited workers flew to test feeders in the direction indicated by the dance rather than the direction from which the dancer had returned. The more recent experiments with an effective model bee, which certainly did not convey location specific odors, abundantly confirm that information about distance and direction can be conveyed from the dancer to her sisters.

The accuracy of this distance and direction information has been studied by von Frisch (1967) and more recently by Towne and Gould (1988). The basic approach was to set out test feeders with the same odor as that associated with a rich source of concentrated sucrose and, after removing the original source of food about which bees had been dancing, to measure how many recruits arrive at the test feeders. In both von Frisch's original experiments and these more carefully controlled tests, the majority of the recruits went to feeders in approximately the same direction and at approximately the same distance as the location indicated by the dances. There is, however, considerable variation and the situation is complicated by the possibility that the odors marking the location of the original feeder or the test feeders may diffuse widely enough that bees are attracted to them even though they may not have flown very accurately to the distance and direction indicated by the dances they have followed. In general terms, it seems that the direc-



tional indication is accurate within approximately plus or minus 20–30 degrees and the distance indication perhaps plus or minus 10 or 15 percent. Evidently the finding of the exact location requires response to the odors conveyed at the time of the dancing. But the symbolism of communicating direction and distance is very significant, even though its accuracy is not all that one might ideally desire.

One misunderstanding of the dance communication of honeybees that is very widespread is the belief that it is rigidly linked to food. As mentioned above, the dances are also used to communicate about water needed to cool the colony by evaporation, but water can be viewed simply as a very dilute sugar solution. Waxy materials are sometimes collected and their location indicated by waggle dances. But the most enterprising use of the dance communication system occurs when bees are swarming. Although these dances were discovered many years ago by Lindauer (1955), ethologists have devoted very little attention to them despite their implications concerning cognition.

Swarming occurs when a colony of honeybees increases to the point that the hive is crowded. Workers then feed some larvae a different sort of food, which causes them to develop into queens. Under ordinary conditions the bees also prepare to swarm, and part of the behavioral changes that accompany this sort of preparation is a change in the searching images of the older workers that have previously been gathering food. They now begin to investigate cavities. As new queens develop, the older queen stops laying eggs and usually moves out of the hive along with a large portion of the workers. Initially these aggregate in a ball of bees clinging to the surface of the hive or to vegetation. In normal bee keeping practice the beekeeper either enlarges the hive at the first sign of swarming so that the colony can grow further or else he provides a new hive immediately below the swarm. A beehive is an ideal cavity and the bees usually move directly into it.

Many colonies of bees flourish away from carefully tended apiaries, and when they swarm no beekeeper provides an ideal cavity in the immediate vicinity. Under these conditions many of the older workers, rather than searching for flowers or other sources of food begin to search widely for cavities. Often they must search over a very large area, crawling into innumerable crevices in trees, rocks, or buildings. Their central nervous systems must recognize a searching image for an appropriate sort of cavity. A cavity is of course something totally different from food, and these workers that now search for cavities have never in their lives done anything of the kind. Swarming ordinarily occurs at intervals of many months, and workers live only a few weeks during the

warmer months when they are active. While the queen may have participated in swarming many months before, the workers have never experienced anything remotely like the movement out of the old hive and the aggregation of thousands of bees in the open.

It is not easy to find an appropriate cavity. It must be of roughly the right size and have only a small entrance near the bottom. It must be dry and free from ants or other insects. In one of the few investigations that has followed from Lindauer's discovery Seeley (1977) has studied how the scout bees investigate cavities. He established colonies on small islands where no suitable cavities were present and induced swarming by the simple procedure of shaking the queen and numerous workers out of the old hive and leaving them to their own devices in the open air. He then provided experimental cavities of different types at some distance. The workers found these and eventually induced the colony to occupy one of them. In their preliminary visits these workers crawled back and forth through most of the interior of the cavities and spent considerable time investigating them.

When Lindauer studied swarming bees he observed that workers carried out waggle dances on the surface of the swarm. These are similar in some ways to dances that are occasionally carried out on a horizontal surface in front of the hive entrance. When bees are dancing on a horizontal surface in the open they point directly toward the food or whatever the dances are about. The symbolic transfer to gravity with upward pointing dances meaning toward the sun apparently does not occur when the dancer and any of her sisters who follow the dances are on a horizontal surface and can see the sun.

The waggle dances executed on the swarm indicate the distance, direction and desirability of the cavity which the dancer has visited. This means that the dance communication system, with all its symbolism, is employed in this totally unprecedented situation. The same code indicates the location and quality of something as different from food or water as one can imagine. Worker honeybees that have been gathering nectar from flowers during the past few days, and which may even continue to do so to provide food for the swarm, utilize the totally different searching image of a dry, dark cavity of appropriate size to guide both their searches for such cavities and their communication about one that they have visited. If we accept specialized communicative behavior as suggestive evidence of thinking on the part of the communicating animal, we may infer that these worker bees think about either food sources or cavities, according to the needs they have perceived at the time.

In his classic experiments during the 1950s, Lindauer discovered that the waggle dances executed on a swarm lead to a group decision on the part of the colony about where they should move to establish a new colony. Ordinarily dozens of scout bees that locate cavities dance on the swarm about different locations. Furthermore, the intensity of the dances is correlated with the quality of the cavity. Small, damp, or ant-infested cavities produce only a few feeble dances whereas others that are dark, dry, and of suitable size lead to prolonged and vigorous waggle dances. Since different scouts have visited different cavities, a wide variety of locations are described by the numerous dances that go on over the surface of a swarm.

Lindauer spent many hours in laborious observations of the dances on the surface of numerous swarms, climbing ladders, or doing whatever was necessary to reach a suitable observation point. He found that although a wide variety of locations were signaled in the first few hours after a swarm emerged from the original hive, the dances gradually came to represent a progressively smaller number of locations. As time passed, the few cavities described by the dances that were carried out by increasing numbers of bees were those that had originally elicited the most vigorous dances. In other words, the cumulative effect of extensive dance communication was a progressive reduction in the number of cavities described. And those that continued to be danced about were the best ones available.

In further experiments Lindauer varied the suitability of particular cavities. If their quality was lowered, the dances became less enthusiastic; and in some situations at least, dances about other cavities became more numerous. This process of repeated dancing about the more desirable cavities went on for a few days, and finally almost all dances were about a single cavity. After this had been going on for several hours, a different sort of behavior occurred, which Lindauer describes as a "buzzing run." The bees making these buzzing runs moved for fairly long distances over the swarm while emitting a buzzing sound. When this had been going on for some time the swarm took wing and flew fairly directly to the cavity that had been described by the concentration of enthusiastic dances over the past day or so.

These dances on the swarm lead to a sort of consensus whereby the colony selects out of many possible cavities the one that has been judged by the scout bees to be the best. There seem to be adaptive advantages to prolonging this process of evaluation, because cavities may change their desirability as conditions change. For example, one that has been dry in good weather may be damp on a rainy day. Thus it seems that the

bees do not reach this crucial decision until dancers have been, so to speak, singing the praises of a particular cavity for a considerable period of time. Many factors probably play a role in the evaluation of cavities by individual scout bees. In addition to size, dryness, and a dark interior with a small opening, distance from the original colony is important. It seems that other factors being equal the bees prefer a cavity a few hundred meters from the old colony. This presumably has the advantage of avoiding competition for food sources with the thousands of bees that remain in the original cavity and continue to search vigorously for food.

Although we can only speculate about what, if anything, these dancing bees and their sisters who follow the dances on swarms are thinking, their vigorous communication suggests that they are thinking about a suitable cavity, perhaps similar to the one from which they have recently emerged. Lindauer also observed another feature of the communication on swarms that has significant implication for a cognitive interpretation of the communicative behavior. In the first day or two, after the swarm had emerged and a number of different cavities were being described by various returning scouts, one might suppose that the less desirable cavities dropped out of the communication process because scouts that had visited them simply stopped dancing, while those returning from the better cavities continued. Yet the individual bees return repeatedly to the cavities after a bout of dancing, so that the same individuals continue to describe the cavities they have located over many hours or even a few days.

By marking individual dancers, Lindauer discovered that something even more interesting was going on. Bees that had visited a cavity of mediocre quality sometimes became followers of more enthusiastic dances than their own. Then some of them visited the better cavity they had learned about as followers of vigorous dances, returned, and danced appropriately with respect to the superior cavity they had now visited. Lindauer was only able to observe this in a handful of cases, and it is not clear how large a role this change of reference of the dances of individual bees plays in the whole process of reaching a group decision. Nevertheless the fact that any bees change from dancing about one cavity to another, after switching roles from dancer to follower, means that the whole process of communication by means of waggle dances is not a rigid one linked tightly to the stimulation received during visits to the first cavity a particular individual has located. It seems reasonable to infer that under these conditions bees are thinking about cavities, and are able to change their "allegiance" from one they have discovered themselves to a better one they have learned about as recipients of sym-

bolic information from the dances of one of their sisters. Unlike the weaver ants studied by Hölldobler and Wilson, however, Lindauer did not see any signs of chain communication. When dancers changed the cavity about which they danced they did so only after visiting the second cavity.

All this communicative versatility certainly suggests that the bees are expressing simple thoughts, as I have argued elsewhere (Griffin 1981, 1986). One significant reaction to von Frisch's discovery was that of Carl Jung (1973). Late in his life he wrote that, although he had believed insects were merely reflex automata,

this view has recently been challenged by the researches of Karl von Frisch; . . . bees not only tell their comrades, by means of a peculiar sort of dance, that they have found a feeding place, but they also indicate its direction and distance, thus enabling beginners to fly to it directly. This kind of message is no different in principle from information conveyed by a human being. In the latter case we would certainly regard such behavior as a conscious and intentional act and can hardly imagine how anyone could prove in a court of law that it had taken place unconsciously. . . . We are . . . faced with the fact that the ganglionic system apparently achieves exactly the same result as our cerebral cortex. Nor is there any proof that bees are unconscious.

## *Deception and Manipulation*

**I**n the previous chapters animal communication has been considered as a straightforward transmission of information from one animal to another, and it has been tacitly assumed that this information is reasonably accurate. That is, when one animal, the sender, emits a signal, this signal is taken as some indication of its intentions, or at least of its disposition to behave in a certain way, that can be reliably interpreted by one or more other animals, the receivers. (The terms “actor” and “responder” are sometimes used instead of “sender” and “receiver”; but the latter are preferable because they do not imply anything about behavior of the receiver, which may not react at all.) I have emphasized the possibility that the production of communicative signals may be consciously intentional, that the sender may want to transmit information to the receiver because it wishes to affect the receiver’s behavior in some way. Inclusive behaviorists have avoided any such inferences, preferring to concentrate attention on the functional effects of the communication, especially its contribution to evolutionary fitness, rather than on any mental experiences of either sender or receiver.

Dawkins and Krebs (1978) in an eloquent and influential paper have argued against what they call the classical ethological analysis of animal communication, which emphasizes cooperation between individual animals facilitated by transmission of accurate information about the sender’s dispositions to behave in particular ways. Instead they emphasize the struggle between individuals, both between members of the same and different species. This emphasis stems from a strong preference for the “picture of an animal as a machine designed to preserve and propagate the genes that ride inside it” as argued forcefully by Dawkins (1976). Dawkins and Krebs interpret communicative signals as means to manipulate others, rather than to inform them. From this perspective it seems likely that the information transmitted by communicative signals is often inaccurate, and serves to misinform the receiving animal.

As pointed out by Hinde (1981) the difference between the two approaches is not as fundamental as Dawkins and Krebs assert. Ethologists studying animal communication have almost always considered that communicative behavior is adaptive, that it has resulted from natural selection, and that it often enables one animal to alter the behavior of another to the former's advantage. The difference is one of emphasis: Dawkins and Krebs conclude that most animal communication has been selected for its effectiveness in manipulating others for the sender's benefit, while other ethologists point out that mutual benefits to both sender and receiver are widespread, as discussed by Smith (1986). For, in the long run, "cheating" by transmitting inaccurate information works only if most signaling is reasonably accurate. Otherwise receivers will be selected to ignore, or even perhaps "see through" the inaccurate, manipulative signaling, as reviewed by Wiley (1983). The evolutionary significance of honest and dishonest signaling has been extensively discussed by ethologists, and recently reviewed by Guilford and M. S. Dawkins (1991).

Many ethologists and behavioral ecologists have found the approach espoused by Dawkins and Krebs a congenial one. One reason is that it tends to appear consistent with the "selfish gene" approach to animal behavior, but another possible reason may be that it seems to avoid the need to suppose that communicating animals might consciously mean what they say. This viewpoint has been advanced as a reason to reject the suggestion that animal communication could serve as an effective source of data about animal thoughts or feelings. The fact that animal signals sometimes convey inaccurate information detrimental to the receiver but beneficial to the sender complicates their interpretation, since we must consider that they may be either accurate, inaccurate, or some mixture of the two. But in either case the signals are expressions of something going on within the sender's nervous system, and they may convey the sender's feelings or thoughts whether these are cooperative or competitive, honest or devious. In fact, deceptive communication may be more rather than less likely to require conscious thinking than accurate expression of what an animal feels, desires, or believes. More recently Krebs and Dawkins (1984) have modified and elaborated their analysis by adding "mind-reading" to their evolutionary analysis of animal communication, as discussed in chapter 1.

This chapter will review several cases where animal communication does not appear to convey accurate information, and where the flexible versatility displayed suggests conscious thinking on the part of sender, receiver, or both. This subject has been reviewed in a symposium edited

by Mitchell and Thompson (1986), and I will draw on several specific examples of deceptive behavior described in that volume.

Some discussions of deceptive behavior include in this category morphological mimicry, in which the colors or shapes of animals resemble dangerous or inedible objects, as well as cases where their behavior conveys inaccurate information. Clearly the former type is of little or no interest in relation to the possibility of conscious deception. Animals ordinarily have no choice about their body coloring, although in a few cases, such as chameleons, chromatophores in the skin are under nervous control and the animal does change its color to some extent to match its background and make itself less conspicuous (Winkler 1968). This behavior seems not to have been studied thoroughly enough, however, to provide much indication of the degree to which it might entail conscious thinking. Cryptically colored moths tend to land selectively on surfaces where they will be less conspicuous (Kettlewell 1955, Kettlewell and Conn 1977, Sargent 1981, Partridge 1978), but it is difficult to tell from available evidence how much versatility is required in making these selections of landing places.

Some animals make definite efforts to display patterns that look like dangerous objects, although they have no control over the presence of these patterns, they do expose them on appropriate occasions. For example, many species of butterflies and moths have eye spots on the dorsal surfaces of their hind wings which look remarkably like two eyes. These are not visible when the wing is folded, but are suddenly exposed by spreading the wings when the moth is attacked. Experiments by Blest (1957) showed that these startling displays often scare off attacking birds. When the scales forming the pattern on a moth's wings were removed, it spread its wings normally, but the display had a much reduced effect. Moths without eyespots elicited only about one quarter as many escape responses from birds as normal moths. Blest was also able to show similar effects when artificial eye-like patterns were presented to birds along with mealworms. But we know too little to judge how flexible and versatile these antipredator displays of moths actually are.

### Firefly Communication and Deception

The extensive investigations of Lloyd (1986) have revealed that these luminescent beetles engage in fantastically complex social communication mediated by temporal patterns of their self-generated flashes. Numerous species of fireflies are very similar morphologically, so much so that entomologists can often identify them more readily by their flash-



ing patterns than from examination of captured specimens. Of the 130 species Lloyd has studied under natural conditions, the most intriguing patterns have been analyzed in the American genera *Photinus* and *Photuris*. Male *Photinus pyralis* typically begin to search for females by emitting a half-second flash about every six seconds while flying near bushes where females are likely to be perched. A responsive female waits about two seconds and then emits her own half-second flash. The male turns toward her and they exchange similar flashes until he reaches her position, where mating often takes place. Females usually find a mate within a few minutes, and then return to their burrows to lay eggs. Males, on the other hand, may search for several nights before finding a responsive female of their own species.

Life is complex and hazardous for male *Photinus pyralis* fireflies. Their flashes are answered only about half the time by females of their own species. At other times very similar answering flashes come from females of the larger genus *Photuris*, which are predatory and may catch and eat males that come too close. Yet the predatory “femmes fatales” actually capture only about 10–15 percent of the males that approach them, suggesting that at close range the male *Photinus pyralis* can detect differences between the flashes of conspecific females and those of the predatory *Photuris*. It is also possible that other information such as species-specific odors might play a role in these close encounters. Sometimes the predatory females also fly aggressively towards potential prey and capture some in this way.

This sounds complicated enough, but the actual situation is much more intricately hazardous for the males. Several other species of fireflies are often present flashing in somewhat different patterns. And even one well studied species such as *Photinus pyralis* changes its flashing drastically under some conditions when aggressive mimics are active. Sometimes several males approach a female but land far enough away that escape is possible if she turns out to be a femme fatale. They seem to be probing with their light flashes to determine from her responses whether she is a conspecific female or a dangerous aggressive mimic. In this situation Lloyd found some indication that males may mimic flashing signals of predatory fireflies, as though to deter rivals long enough to reach a responsive female themselves.

Unfortunately we do not know enough about the histories and experiences of individual fireflies to judge how versatile all this communicative interaction actually is. They are not readily raised in captivity and studied under controlled conditions, so that it is difficult to determine whether their behavior varies in response to changing circumstances, or

whether each firefly has a relatively constant pattern but such patterns vary widely among individuals of the same species. There is certainly great variability and complexity, but not enough is yet known to distinguish random variation from systematic and possibly rational, even Machiavellian, competition. It has been traditional to assume that insects behave in rigid, stereotyped ways that are genetically predetermined. But recent advances in our understanding of insect social behavior have provided abundant evidence that this view may well be a serious oversimplification.

### Mantis Shrimps

Mantis shrimps of the genus *Gonodactylus* are predatory marine crustaceans equipped with appendages that serve, in different species, as clubs or spears. They occupy cavities and burrows in coral reefs and where they are protected from predators. They use cavities as ambushes from which to seize prey, and for mating and egg-rearing. Cavities are essential for survival, and mantis shrimps often fight over them (Caldwell and Dingle 1975). Larger animals can usually evict smaller ones from cavities, but much of this fighting is ritualized posturing and gesturing. Although they can seriously damage each other, they seldom do so (Dingle and Caldwell 1969). Experiments by Caldwell (1979, 1984, 1986) with adult *G. festai* 40 to 47 mm in length demonstrated that they can recognize other individuals of their species by chemical cues. They avoid empty cavities with the individual odor of a mantis shrimp that has defeated them in a previous encounter, but enter cavities containing the odor of one they have bested. Many encounters involve a sort of bluffing, and as Caldwell puts it, they are able both to recognize other individuals and to remember their "reputations" as fighters.

It used to be taken for granted that individual recognition was impossible for invertebrate animals, but this relatively complex behavior is typical of the surprises that have resulted from detailed investigations of ethology. Yet Caldwell is also typical of inclusive behaviorists in closing his review of these ingenious and revealing experiments with the following disclaimer:

The use of reputation and bluff in stomatopods should not be viewed as conscious acts. Rather, they are the product of natural selection operating on probabilities of performance and response. The selective equation has balanced over many generations the costs and benefits of generating, as well as accepting or discounting, signals that correlate with the probable outcome of a contest. The

resulting product is further tuned by experience and by the degree to which information so derived is available and accurate. I hope that by demonstrating the occurrence of such supposedly complex mechanisms as reputation and bluff in relatively simple animals such as stomatopods, I can suggest the existence of similar processes producing “deceptive” interactions in more sophisticated animals whose sensory and integrative capacities make objective analysis much more difficult. (Caldwell 1986, 143)

This is a prime example of the strong inhibiting effect of inclusive behaviorism. Adaptiveness is a completely separate matter from the possibility of conscious thinking. Because mantis shrimp are crustaceans a few centimeters in length, it is assumed *a priori* that they cannot possibly be conscious. Even when they are shown to engage in moderately complex and versatile behavior, these data are forced into the procrustean bed of mindless automatism. Yet mantis shrimp have well-organized central nervous systems, and while their neurophysiology has not been studied in detail it is unlikely to be very different from that of crayfish, which have all the basic mechanisms of synaptic interactions that are found in the central nervous systems of all complex animals (Bullock and Horridge 1965, 1187–89; Schram 1986).

The central nervous system of a mantis shrimp is larger than that of a bee, and it is well known that honeybees and other social insects display a variety of versatile behavior patterns, including symbolic communication, as discussed in chapter 9. It is quite reasonable to speculate that mantis shrimps may experience very simple conscious feelings or thoughts about the fights by which they gain or lose the cavities that are so important to them and the antagonists whose odors they learn to recognize from previous encounters. Perhaps they do no more than feel fearful on sensing the odor of a larger shrimp that has defeated them previously. But we have no firm basis for dogmatically denying any subjective experience at all when behavioral evidence suggests versatile adaptation of behavior to challenges that are important to the animal itself.

### Deceptive Alarm Calls

Many animals have calls that signal danger from predators, and these sometimes differ according to the type of predator, as in the case of the vervet monkeys and domestic chickens discussed in chapter 8. The responses of animals that hear alarm calls are usually to flee from the immediate area, so that the possibility exists that a sender might use alarm calls to frighten others away from a place the sender would like to have

to itself. Because it is vitally important to escape predators announced by alarm calls, such escape responses are likely to be resistant to habituation, as Cheney and Seyfarth found to be the case in their experiments described in chapter 8.

Other cases of this type have been observed in mammals, birds, and even ants, as reviewed by Munn (1986a). Most of these instances have not been studied in sufficient detail to tell us how consistently false alarms are sounded or to provide very helpful hints as to the likelihood that this behavior is carried out with conscious intent. Recently, however, Moller (1988) has demonstrated that great tits (*Parus major*) give false alarm calls when no danger was threatening to disperse sparrows that were monopolizing a concentrated food source. When food was scarce and the tits had to feed at a high rate in winter, they also gave false alarm calls to frighten other birds of the same species away from restricted and desirable food sources.

A striking instance of what appears to be complex deceptive behavior by a hummingbird has been reported by Kamil (1988, 257–58). A male Anna's hummingbird named "Spot" because of a white spot on his face had detected a mist net in his territory because a heavy dew had made the black threads conspicuous.

Spot saw [the net] immediately. He had flown along it, and even perched on it. Experience had taught us that once a hummingbird has done this, it will never fly into the net. . . . Suddenly an intruding hummingbird flies into the territory . . . and begins to feed. Male Anna's hummingbirds are extraordinarily aggressive animals. Usually they will utter their squeaky territorial song and fly directly at the intruder, chasing it out of the territory. But that is not what Spot does. He silently drops from his perch and flies around the perimeter of the territory, staying close to the ground, until he is behind the other bird. Then he gives his song and chases the intruder—directly into the mist net.

Although Yoerg and Kamil (1991) argue against inferring conscious intention in animals, Spot's behavior is certainly suggestive of intentional planning.

In the course of detailed studies of mixed flocks of neotropical forest birds, Munn (1986a, 1986b) has documented a type of false alarm calling that is highly suggestive of intentional deception. He studied two groups of birds in the Amazon basin of Peru that live in permanent mixed-species flocks, one group is mostly found in the forest canopy, 15–45 meters above the ground, the other in the understory below 15 meters. While several species sometimes join these flocks, mated pairs of four to ten species form the core of the flock and remain with it most of

the time. The understory and canopy flocks may even join together at times and occasionally as many as 60–70 species may be assembled in a single flock.

In the understory flocks one species, the bluish-slate antshrikes *Thamnomanes schistogynus* tend to lead the others when the flock moves for distances of more than about 20 meters. They give loud calls which seem to help maintain flock cohesion. In the canopy flocks the white-winged shrike-tanagers *Lanio versicolor* play the same role as the lead species. These two species spend more time perched than the others, and obtain most of their food by flying out to snatch insects off leaves and from the air; the others spend more time searching for and flushing insects from the forest vegetation. The lead species in both canopy and understory flocks also serve as flock sentinels; they are almost always the first or even the only members of the flock to give loud alarm calls when they see one of the several hawks of the genera *Micrastur*, *Accipiter* and *Leucopternis* that are serious predators on these insectivorous birds.

On hearing these alarm calls the other members of the flock look up, freeze, dive downward, or move into thick vegetation. This division of labor in mixed species flocks seems to be mutually advantageous. The leader-sentinels obtain at least 85 percent of their food from insects flushed by other species, and in return they provide timely warning of danger from hawks so that the other birds can spend more time searching for edible insects. Typically the sentinel-leaders sit near the center or beneath a group of actively foraging members of the flock and when an insect is flushed by one of the latter, they fly out and downward in hot pursuit of the quarry. Since they are faster and more acrobatic fliers they often catch the insect first.

In the course of these multi-bird tumbling and competitive chases of insect food, the sentinel-leaders often give hawk alarm calls very similar to those elicited by real hawks. Playbacks of alarm calls recorded either on sighting a real hawk or in one of these competitive insect chases clearly startle other flock members. The sentinel-leaders give alarm calls significantly less often when they are the only bird chasing an insect than when others are also pursuing it, indicating that the deceptive alarm calling is employed primarily when it is helpful in competition for food, and not whenever insects are being chased.

Munn (1986a, 174) concludes by interpreting his observations in terms of possible thinking by the birds involved: "Certain facts suggest that some amount of thinking is involved both in sending and receiving the alarm call. That the sender thinks about what its call implies is suggested by one occasion in which a *Thamnomanes schistogynus* began to

give the false alarm call as it flew out after a falling insect that was being chased by another bird, but once it became clear that the other bird had captured the insect, the calling antshrike immediately graded its call into a wider-frequency nonalarm rattle call, which functions like a rallying call for other birds. The bird apparently realized that the alarm call was no longer appropriate and switched to the nonalarm call in mid-vocalization. Additionally, the fact that both sentinel species use the false alarm calls more frequently when feeding fledglings might suggest that they are 'saving' this trick for a situation in which they are genuinely desperate for extra food. The behavior of receivers suggests that they recognize that one potential meaning of the alarm calls is the approach of a predator. These birds are not simply startled by an alarm call—rather, often they look in the direction of the call. This reaction is especially obvious when birds already in thick cover jerk their heads quickly and look in the direction of an alarm. This looking implies that alarm calls are interpreted as meaning something more like 'hawk!' than like 'jump!'"

Inclusive behaviorists can of course interpret the results of Munn's observations in terms of natural selection for behavior that increases the birds' evolutionary fitness or learned behavior reinforced by food. But the flexible versatility with which false alarming occurs primarily under appropriate conditions suggests that these birds are intentionally deceiving their competitors. As in other cases of this sort, the two interpretations are not mutually exclusive. Behavior reinforced by either learning or natural selection may also entail conscious intent. Indeed the capability of such conscious intention may be an important part of what is selected or reinforced.

### Predator Distraction Displays

When animals are frightened by the close approach of a larger creature they sometimes exhibit striking forms of behavior that involve ceasing most bodily activity, becoming immobile, or acting as though badly injured or even dead. The adaptive function of most instances of such behavior is unclear, for it is difficult to understand why a predator about to eat an animal would be deterred by its suddenly becoming immobile and ceasing all efforts to escape. But some of these displays are remarkable in the degree to which they simulate death. Burghardt (1991) discusses the death simulation of the hognosed snake (*Heterodon platirhinos*), which writhes erratically, defecates, turns over and remains quiet with an open mouth, tongue hanging out, even bleeding at the

mouth and without appreciable breathing. This bizarre behavior has typically been viewed as an uncoordinated, instinctive response. But Burghardt reviews old and new evidence that even in this state of apparent death, the hognosed snake watches the animal that stimulated it. If this animal goes away, the snake recovers, and it remains in the state of death simulation longer if a human intruder looks at it. Thus even in an extreme state of a death-simulating display, the snake monitors the animal that stimulated it to perform this display.

Various birds employ a wide range of antipredator behavior, ranging from direct attacks to maneuvers that tend to deflect an intruder's attention to the bird itself instead of its vulnerable eggs or young, as reviewed by Armstrong (1942) and by McLean and Rhodes (1991). When small birds attack larger predators they often call loudly, dive at the intruder, empty on it the contents of the stomach or cloaca and sometimes even strike it with the legs or bill. Such attacks are usually quite effective in driving the intruder away, even against hawks that occasionally turn on their tormentors and kill them. An especially significant and suggestive form of deceptive communication takes place when certain ground-nesting birds perform elaborate displays that serve to distract predators that might otherwise destroy their eggs or young. Plovers and sandpipers typically lay their eggs in simple nests on the ground where they are especially vulnerable to predation. Their many and varied types of antipredator behavior, reviewed by Gochfeld (1984), include maneuvers that are more complex and devious than direct attacks. Although their eggs are cryptically colored and resemble the substrate on which they are laid, many plovers and sandpipers respond to intruders with specialized distraction displays.

The most striking type of predator distraction behavior is displayed by several species of small plovers, such as the North American killdeer (*Charadrius vociferus*), piping plover (*C. melodus*), and Wilson's plover (*C. wilsonia*). Killdeer typically nest in open fields, and the piping and Wilson's plovers lay their eggs on sandy beaches. The nest itself is little more than a shallow depression. When a larger animal approaches the nest of a plover, one common response is for the incubating bird to stand up and walk slowly away from the nest for a few meters. Then it may begin calling, in the case of the piping plover a plaintive peeping that has given the bird its name. Often the parent bird then walks or flies closer to the approaching intruder and begins a conspicuous display. This behavior contrasts with the ordinary behavior of flying directly away from a frightening intruder when the bird has no eggs or

young. The displays themselves vary widely, but usually involve exposing conspicuous patterns and moving in atypical ways.

One type of display is called a crouch run; the bird holds its body close to the ground, lowers its head, and runs in a way that makes it resemble a small rodent such as a vole. Sometimes the plover even emits rodentlike squeaks during these crouch runs. Most predators that would be likely to eat plover eggs or chicks are probably also likely to pursue a vole, so that the rodent-like crouch run seems likely to divert attention from a search for eggs or plover chicks. Similar displays have also been observed in a small passerine bird by Rowley (1962). At times plovers threatened by an approaching intruder settle down into a small depression in the sand as though incubating eggs. Such false incubation may lead a predator to search at the empty depression rather than the actual nest.

Other common distraction displays involve postures and movements that render the bird conspicuous or cause it to appear injured. The tail may be spread abnormally, one or both wings may be extended or even dragged on the ground as the bird moves over an irregular course. In the extreme form of this display, called the broken wing display, the bird falls over and flops about as though badly injured, perhaps with a broken wing. It looks just like a bird that has been winged by a hunter's shot. Predators are especially alert for signs of weakness or injury in potential prey, and these displays must make the bird appear especially vulnerable.

The customary explanation of these distraction displays has been that the bird is in severe conflict behavior, being motivated both to flee and to attack, with the result that it is thrown into a state bordering on an uncoordinated convulsion (Skutch 1954; Simmons 1955; Armstrong 1949). The strong influence of inclusive behaviorism has led most ornithologists and ethologists to deny emphatically that a bird might intentionally attempt to deceive a predator and lead it away from its young. For example, Armstrong (1949, 179) asserted that "it is ludicrous to suppose that injury-simulation arose through birds deciding the trick was worth trying." Although Armstrong was speaking of evolutionary origins, he and other ornithologists seem equally certain that the birds do not individually display with the intention of leading the predator away. One reason to question whether the displaying birds are consciously trying to lead a predator away is the fact that they sometimes continue displaying even after it has killed their young, as described by Drieslein and Bennett (1979). Such continuation of distract-



tion display after the predator has taken the eggs or young may indicate that the bird is not consciously intending to lead the predator away. Although obviously not completely rational, this continuation of the display may be comparable to other emotional expressions that are carried on after they can no longer achieve a desired effect.

Broken wing displays provide an especially suitable situation where new observations and experiments can throw some light on the possibility that the birds are acting intentionally. Not that any evidence yet contemplated can settle such a question conclusively; but certain features of the bird's behavior strengthen the plausibility of inferring conscious intent. Such an analysis has been carried out by Ristau (1983a, 1983b, 1983c, and 1991) with piping plovers and Wilson's plovers nesting on beaches in Virginia and Long Island. Almost all data that are available about the details of predator distraction displays have so far come from encounters with human intruders, because it is only rarely possible to observe natural encounters between plovers and mammalian predators. The few observations that have been reported indicate that the predator distraction displays in response to natural predators are very similar to those elicited by human intruders who approach a nest where plovers are incubating eggs or areas where young chicks are present. Armstrong (1942, 89–91) reviewed several observations of an otter, foxes, weasels, dogs, and cats being led away from young birds by parents acting as though injured. Sullivan (1979) observed a black bear being successfully lured away by a blue grouse hen. Pedersen and Steen (1985) analyzed the effectiveness of predator distraction displays of ptarmigan. And Brunton (1990) observed that distraction displays of killdeer were almost always effective in leading potential predators away from eggs or chicks.

Sonerud (1988) has recently described direct observations of foxes that apparently "saw through" the injury-simulating displays of grouse and responded by searching the immediate vicinity for grouse chicks rather than following the displaying adult. He develops a theory that when small mammal prey is abundant, young foxes do not learn that distraction displays mean young birds nearby, but that in years when small mammals are scarce, foxes are more likely to learn that such displays are a sign of available prey in the vicinity. Thus there may well be a sort of cognitive interaction between parent birds and predators by which distraction displays are reduced or eliminated in situations where the predators are clever enough to interpret them as signs of edible eggs or chicks nearby rather than an injured bird worth pursuing.

One indication that these displays are something other than chaotic

convulsions is that the bird frequently looks at the intruder. Even when moving away it repeatedly turns its head and looks back. During broken-wing or other distraction displays the plover does not ordinarily stay in one spot but moves slowly and somewhat erratically over the ground. If the intruder does not follow, the bird typically stops displaying and moves to a different position where it repeats the display, often with increased vigor. Significant indications of intentional, rather than chaotic or unplanned, displaying also resulted from Ristau's analysis of the spatial relations between the intruder, the nest or young, and the displaying bird. If the displays result from a simple mixture of motivation to attack and to flee, one would expect the parent bird to approach the intruder, then withdraw, and perhaps approach and withdraw alternately as one or the other motivation came to predominate. But there would be no reason to expect that the location of the nest would play any significant role in such movements, except that, having come from somewhere near the nest, a plover that simply approached the intruder and then withdrew would often move back toward the nest.

Intruders are ordinarily detected at a considerable distance, and the parent bird usually walks slowly and inconspicuously away from its nest before flying fairly close to the intruder while it is still many meters from the eggs or young. As the intruder comes close, the displaying plover moves a bit faster, and although appearing crippled and easy to catch, it always manages to stay just out of reach. On one occasion a displaying Wilson's plover led me along a beach for about 300 meters with almost constant displays.

When Ristau mapped where the intruder would have been led if it followed the plover throughout its broken-wing displays, she found that in 44 out of 45 cases the intruder was led away from the nest. Since the displays began at positions that varied widely with respect to the line connecting the nest with the initial position of the intruder, some routes might be expected to lead initially a little closer to the nest before continuing off in a quite different direction. But in only 39 of the 45 cases would an intruder have moved closer to the nest at any time while it was following the displaying bird.

Another indication of something other than mechanical and random flopping about in chaotic conflict behavior is the degree to which plovers are selective about which intruders will elicit full-blown displays. They habituate to familiar people, especially on heavily visited beaches. Skutch (1976) and Armstrong (1949, 1956) both observed that when cattle or other hooved animals approach their nest, instead of behaving as though injured, plovers sometimes stand up conspicuously, close to

the nest with spread wings, and may actually fly directly at an approaching cow. This is sensible behavior, because the danger from cattle is not that they will eat the eggs but that they may step on them.

Ristau (1991) carried out systematic experiments to analyze this selectivity of response to different kinds of intruder by having human intruders behave in two clearly different ways towards an incubating plover. One category, termed "dangerous" intruders, walked to within two meters or less of the nest, looked about, and acted as though searching. They must have appeared to the parents as more likely to destroy the eggs than others, designated "safe" intruders, who walked past the nest tangentially but did not approach closer than 12 to 32 meters. The two categories of human intruders dressed as distinctively as possible. Both before and after being exposed to one to four such dangerous and safe approaches the plovers were tested by having the previously safe and dangerous intruders walk past at a constant, moderate distance.

In 25 out of 31 tests the plovers reacted more strongly to the intruder who had previously acted dangerously than to the one who had played the "safe" role. Stronger responses entailed looking up or moving away from the nest at a greater distance, staying off the nest longer, and performing more active displays. In three of the remaining six experiments there was no appreciable difference. In the other three cases the response was the opposite of what would be expected if the birds had learned which person was the more likely to threaten the nest, that is, the response was stronger to the safe intruder than to the one who had behaved dangerously. Thus in the great majority of these tests the plovers learned in the course of a few exposures to safe and dangerous intruders which one posed the greater threat and called for the more vigorous response.

In other experiments Ristau had human intruders either look at the nest or turn their heads and gaze in the opposite direction as they walked past at a moderate distance. Again, the plovers reacted more strongly to the distinctively dressed persons who were looking directly at their nests than to those that looked the other way. All these observations and experiments indicate rather strongly that plovers learn quickly which types of intruder are dangerous and respond more strongly to them than to others that have previously behaved in a less threatening manner. Byrkjedal (1991) has concluded that conflict of motivations is not an adequate explanation of nest-protection behavior in golden plovers. They and other birds performing predator distraction displays may well be thinking in simple rational terms about balancing the risks of nest predation against the effort and risks involved in leaving the nest

and carrying out distraction displays, which may be wasted effort at best, or under adverse weather conditions may lower the chances that the eggs will develop normally.

### Deceptive Behavior of Monkeys and Apes

Several other examples of deceptive or manipulative communication are described in the book edited by Mitchell and Thompson (1986). Of particular interest is an illustrated English translation of the paper by Ruppell describing deceptive use of an alarm call by a mother arctic fox whose young were snatching food and kept the mother away by urinating at her. Elephants (chapter 11) and dogs (chapter 12) show clear evidence of deceptive behavior, although it is very difficult to be sure how much conscious intent is involved. With apes, however, the circumstantial evidence of conscious deception is considerably stronger, as described in detail by Miles (chapter 15) for an orangutan who had been trained to use a simple form of sign language, and especially by de Waal (chapter 14 and de Waal 1982), whose longterm studies of captive chimpanzees documented numerous cases of deceptive behavior. Especially revealing were de Waal's observations of subordinate males who often sought, and sometimes obtained, sexual intercourse with adult females, but only when the more dominant adult males did not see them copulating. Both partners in these surreptitious liaisons acted furtively and seemed clearly to be keeping out of sight of the dominant males. If discovered in the act of close sexual advances, such a subordinate male hastily covered his erect penis with his hands. This is in effect deceptive noncommunication.

Byrne and Whiten (1988), Whiten and Byrne (1988), and Whiten (1991) have reviewed published descriptions of apparently deceptive behavior in many species of primates, and they have suggested how this subject can be more adequately studied in the future. They emphasize the degree to which even experienced primatologists have been inhibited, or even embarrassed, about reporting behavior that suggests conscious deception. The review by Whiten and Byrne is followed by numerous commentaries from other scientists and scholars, some of whose criticisms demonstrate how strongly the residual influence of behaviorism still limits acceptance of overwhelming circumstantial evidence that primates are quite capable of what Whiten and Byrne call "tactical deception." Yet in their reply to comments on their paper they deny that they are concerned with the "phenomenal worlds" of the animals they study. The behavioristic taboo still lingers on.

On balance, it seems clear that on many occasions animals communicate inaccurate information or intentionally *avoid* conveying certain types of information to others (Cheney and Seyfarth 1988, 1990a, 1990b, 1991). In many cases the versatility of deceptive or misleading behavior provides even more suggestive evidence of conscious intent than the transmission of reasonably accurate information. Although it is difficult to liken such deceptive communication to involuntary groans of pain, the deceptive tactics of monkeys are often inconsistent. For example Cheney and Seyfarth (1990a) describe how a vervet monkey may emit a leopard alarm call during a territorial confrontation with a neighboring troop. This causes the opponents to flee, but the caller may move into the open himself, contrary to normal, prudent behavior when a real predator is approaching. Intentionally deceptive behavior may thus be executed ineptly, which complicates the task of ascertaining whether it results from conscious planning.

## *Apes and Dolphins*

**T**he Great Apes and the whales and dolphins engage in so much versatile behavior that whole books would be required for each group to document the evidence that suggests conscious thinking. I will therefore select only a few of the most striking examples, with emphasis on communicative behavior that provides compelling evidence about what these animals are thinking and feeling.

The world's largest brains are found in cetacean and not human skulls, and the toothed whales or dolphins have brains that are roughly comparable in size and complexity to our own, although Morgane, Jacobs, and Galaburda (1986) point out that the large cerebral cortex of the cetaceans lacks some of the organizational complexities of the primate cortex. Furthermore these marine mammals produce a wide variety of sounds, and engage in complex and versatile behavior, both when trained in captivity and spontaneously under natural conditions. It is as counterintuitive to deny that they think consciously about some of their activities as it would be to advance such an absurd claim about the Great Apes. One of the best examples of mental versatility displayed by captive dolphins is imitation of both sounds and actions. For example, Herman (1980, 402) summarizes observations by Tayler and Saayman (1973) of a bottle-nosed dolphin (*Tursiops truncatus*) who imitated the behavior of a seal, turtles, skates, penguins, and human divers in its aquarium, employing behavior patterns not seen in this or other dolphins under other circumstances:

The behaviors imitated included the seal's swimming movements, sleeping posture, and comfort movements (self-grooming). The dolphin, like the seal, at times swam by sculling with its flippers while holding the tail stationary. The sleeping posture imitated was lying on one side at the surface of the water, extending the flippers, and trying to lift the flukes clear of the water. The comfort movement mimicked was vigorous rubbing of the belly with the under surface of one or both flippers. Additional imitative behaviors by this dol-

phin included the swimming characteristics and postures of turtles, skates, and penguins. The dolphin also attempted to remove algae from an underwater window with a sea gull feather, in imitation of the activity of a human diver who regularly cleaned the window. The dolphin, while "cleaning" the window, reportedly produced sounds resembling those from the demand valve of the diver's regulator and emitted a stream of bubbles in apparent imitation of the air expelled by the diver. Tayler and Saayman also observed a dolphin using a piece of broken tile to scrape seaweed from the tank bottom, a behavior apparently derived from observing a diver cleaning the tank with a vacuum hose. The scraping behavior of this dolphin was then copied by a second dolphin.

Herman (1980, 406) also describes spontaneous observational learning by dolphins in the large tanks where they are trained to perform a variety of complex gymnastics to entertain spectators:

In some cases, the animals may even train themselves. In one interesting episode illustrating self-training, one animal of the group had been taught to leap to a suspended ball, grasp it with its teeth, and pull it some distance through the water in order to raise an attached flag. This animal was subsequently removed from the show and a second animal in the group was trained in the same task, but learned to raise the flag by striking repeatedly at the ball with its snout rather than by pulling it. This second animal, a female, subsequently died and another female of the group immediately took over the performance, without training, and continued to strike at the ball with the snout. Later when this new female refused to participate in the show during a two-day period, a young male in the group immediately performed the behavior, but grasped and pulled the ball with his teeth, in the manner of the originally trained animal.

During the several days when these dolphins watched their companions and, in so doing, learned the novel sequence of actions, they must have thought about these specialized behavior patterns.

Pryor, Haag, and O'Reilly (1969) and Pryor (1975) describe how a captive rough-toothed dolphin (*Steno bredanensis*) learned to perform a new trick every day in order to obtain food, another sort of enterprising behavior that seems likely to have required at least some conscious thinking. MacPhail and Reilly (1989) have demonstrated that pigeons can learn to discriminate between novel and familiar stimuli, but creating novel and moderately complex actions is a more demanding task. Pending further experiments comparable to those of Pryor et al. it is difficult to judge whether other animals could learn to do this.

The bottle-nosed dolphin is the most commonly trained performer in oceanaria, and it has also been studied most thoroughly by scientists. These and other dolphins emit a variety of sounds, both click trains used

for echolocation and longer duration sounds, usually of lower frequency, by which they communicate; and they can be trained to imitate a wide variety of whistle-like sounds (Richards, Wolz, and Herman 1984). They often produce a medley of sounds when engaged in social interactions, but the physical properties of underwater sounds make it extremely difficult to determine which sounds come from a particular animal when they are close to one another. This is because underwater sounds have much greater wavelengths than the same frequencies in air, and they are attenuated scarcely at all over distances of several meters while being strongly reflected from most surfaces they encounter, including the air-water interface. The sounds emitted by most terrestrial animals are audible to human ears, and a listener can usually judge the direction from which they arrive with considerable ease and accuracy. But underwater sounds cannot be localized nearly so well, even when converted to airborne sounds by hydrophones connected to earphones, primarily because multiple reflections are often at least as intense as the sound waves arriving directly from the source.

One important type of sound emitted by dolphins is the so-called signature whistle, a frequency and amplitude modulated sound that is characteristic of each individual. These were studied in detail by Caldwell and Caldwell (1965, 1968, 1971, 1973, 1979) and Caldwell, Caldwell, and Tyack (1990). The Caldwells were obliged to record them primarily from dolphins that were isolated out of the water, because of the difficulties of separating sounds from various sources underwater. But it was nevertheless clear that more than 90 percent of the whistles were specific to the particular dolphin, and could easily be distinguished from the signature whistles of other dolphins. Tyack (1986) has developed a small and harmless device that can be attached to a dolphin's skin by a suction cup and picks up that animal's sounds much more strongly than those of others in an aquarium tank. This has enabled him to distinguish signature whistles from two animals, Spray and Scotty, that had lived together in the same tank for about seven years. Two types of whistle predominated in their vocal exchanges, and each type was produced primarily, but not exclusively, by one of the two animals. Spray produced 73 percent of one whistle type, while Scotty emitted 74 percent of the other type. Tyack suggests that perhaps the whistles of the other animal's characteristic pattern resulted from imitation. It is even possible that these two dolphins were calling the other by name. But much additional evidence would be needed to demonstrate that such use of whistles as the equivalent of names was actually occurring.

Pryor and Schallenger (1991) have also described how pelagic



spotted dolphins (*Stenella attenuata*) have learned about the purse seines used to surround and capture tuna in the tropical Pacific. The tuna tend to stay below schools of dolphins, which therefore act as markers for the presence of the tuna. These dolphins of the open ocean do not ordinarily encounter any large solid objects, and when this type of fishing was initiated, hundreds panicked and became entangled in the nets. But in recent years they have learned to remain fairly quiet and wait until the crew maneuvers to lower a small portion of the net and allow them to escape. Shortly after escaping from the net the dolphins often leap repeatedly into the air, as though in joyful celebration.

The behavior of the dolphins strongly indicates that they have learned a great deal about the fishing vessels and about what to do when chased by speedboats and surrounded by the net. Experienced fishermen believe that dolphins recognize the fishing vessels from a considerable distance, and that on seeing one they often rest quietly at the surface without conspicuous blowing. If the ship approaches, they may swim rapidly in an apparent effort to keep on its right side; presumably because they have learned that the cranes and other machinery used to handle the nets are usually on the left side. But the tuna fishermen employ speedboats to chase and herd the dolphins into a position where they can be surrounded by the net, which may be as much as a mile in length.

Another sort of versatile behavior of dolphins that suggests conscious thinking is their aiding of other dolphins that are sick or injured. This is relatively uncommon, but it has been observed in detail in several captive groups, and something of the kind occurs occasionally under natural conditions. Aiding behavior is not limited to dolphins, and clear examples in the dwarf mongoose have been described by Rasa (1976, 1983). The instances of dolphins aiding human swimmers presumably result from similar behavior. If a dolphin is visibly weak and sinks below the surface, its companions may swim down and push it from below, lifting it to the surface so that it can breathe air. The dolphins are somewhat selective in this aiding behavior; females and young are much more likely to be assisted in this way, and adult males are sometimes left at the bottom of the tank. Occasionally a dolphin carries this aiding behavior to extremes, such as a mother who carried her stillborn baby for days until it had begun to decompose, or the bottle-nosed dolphin that carried a dead shark for eight days without stopping to eat. Some conscious thoughts seem likely to accompany this aiding behavior, even when the effort is misguided.

Herman (1986, 1987) and his colleagues have approached the question of dolphin cognition by an intensive training program designed to assess the degree to which they can understand not only individual signals but combinations of signals that are related to one another in a manner resembling the grammatical rules of English. This emphasis stems from the widespread conviction that combinatorial productivity based on the use of rule-governed combinations of words constitutes an essential feature of human language. Herman's experiments concentrated on comprehension or receptive competence of dolphins rather than on their ability to produce communicative signals. He trained one female bottle-nosed dolphin, Akeakamai (or Ake), to respond to gestures from a trainer at the edge of the tank, and another, named Phoenix, was trained to respond to underwater whistle-like sounds. Both dolphins learned vocabularies of about thirty-five signals, which included the names of objects in the tank and actions such as toss, swim under, jump over, fetch, and put something in or on top of something else. There were also a few modifiers such as right and left, surface and bottom. A typical combination of signals was RIGHT PIPE TAIL-TOUCH, meaning that the dolphin should touch the floating pipe to her right with her tail.

Both Ake and Phoenix learned to respond appropriately to numerous combinations of these commands, which could be as complex as five-unit sequences such as PLACE BOTTOM PIPE IN SURFACE HOOP, where PLACE IN is a single command. This much was not especially novel, as many dolphins have been trained to carry out sequences of behavior of greater complexity. But in their training, these two dolphins were never presented with more than a small proportion of the possible and meaningful combinations of commands; the others were reserved for tests of their comprehension of the rules that governed the combinations. These rules were similar to those of English, in that the order of the words or commands determined which would be the direct or indirect object, and which modifier applied to a particular name. After the dolphins were responding quite well to these sequential combinations, they were presented with new combinations that they had never received before.

Phoenix responded correctly to 71 to 87 percent of the two- and three-element combinations, diminishing to 60–68 percent for three-to-five-“word” series; and Ake averaged 65 percent correct on all the combinations, doing about as well (74 percent correct) on two- and five-element combinations and less well (56–65 percent correct) on

two-, three-, and four-unit combinations. The overall success of these two dolphins on 405 novel “sentences” was 66 percent correct. While 66 percent correct may not seem very close to perfection, it should be realized that the chance score was very low indeed, since there were a very large number of possible actions among which the dolphins had to choose. Thus these two dolphins had clearly learned not only the meanings of the individual commands but the sequence rules governing which was direct and which was indirect object, and which modifier applied to a given object name.

Schusterman and Krieger (1984) trained two sea lions (*Zalophus californianus*) to respond correctly to 64 and 190 gestural signs displayed by human trainers. Schusterman and Gisiner (1988a, 1988b, 1989) have trained sea lions to comprehend combinations of commands—demonstrating that this ability does not require the brain volume of dolphins or Great Apes. But they and also Premack (1986) deny that this ability to learn combinatorial rules is remotely equivalent to the versatility of human language. They point out that understanding the following two rules would appear sufficient to account for the performance of both Herman’s dolphins and their sea lions (1988a, 346):

1. If an object is designated by one, two, or three signs (an object sign and up to two modifiers), then perform the designated action to that object.
2. If two objects are designated (again, by one to three signs each) and the action is *FETCH*, then take the second designated object to the first.

Comprehension of these rules would seem to require some significant thinking, as discussed by Herman (1988). Of course this comprehension of both individual commands and the meaning conveyed by their sequential relationships falls far short of the rich versatility of human language. But these dolphins and sea lions have learned to comprehend rule-governed combinations of word-like signals. While human languages obviously involve far more than two rules, this is the first demonstration that animals can comprehend *any* syntactical rules at all. In short, two is significantly greater than zero. Furthermore, if dolphins and sea lions think in terms of these rules, they must be capable of thinking in correspondingly complex terms about the relationships between signals and the actions or objects for which they stand. It would be unwise to allow our preoccupation with the quantitatively unique capabilities of human language to obscure the fact that these experiments reveal at least part of what the dolphins were thinking.

The great emphasis on syntactical rules as a fundamental property of language has been announced primarily by scientists and scholars whose native language is English, one of the few human languages where word order provides almost all of the syntax. But in most languages inflection of words is used to convey the grammatical relationships between them, and English does retain a few vestiges of inflection, for example the possessive form of nouns and the different forms of pronouns such as "he," "his," and "him." The fact that so many human languages rely heavily or primarily on inflection of words to convey syntax suggests that inflection may be a more basic and, perhaps, a more easily utilized way to express grammatical relationships. If so, attempts to teach a combinatorially productive language to animals might be more successful if they employed inflection rather than word order.

Fouts (1989) has found by analyzing videotapes of signing chimpanzees that they sometimes "affect the meaning of a sign by modulating it." This has entailed gesturing and gazing at objects of interest while also signing about them. But it is possible that apes might modify the sign itself in ways that would indicate whether it is meant to denote the direct or indirect object, for example. The customary efforts to train apes to standardize their signs would probably discourage such inflection, unless it were specifically encouraged. The Gardners (1989b) have indeed observed that their chimpanzees do modulate the signs they have learned and convey additional meaning by doing so. We may perhaps anticipate that in future investigations the possibility of inflectional syntax will be analyzed explicitly.

A more fundamental distinction between human language and what dolphins and sea lions have accomplished, at least so far, is the ability to switch back and forth between comprehension and production of communicative signals. This is obviously a key attribute of human language, and is an ability that has been attained at least by Kanzi among the Great Apes, as described below. But experiments with marine mammals have not yet even attempted to test whether or not they can learn to comprehend and produce signals interchangeably, and therefore this question must remain open. Obviously dolphins and sea lions cannot be expected to produce human gestures; but Phoenix, who learned to comprehend the rules relating commands presented to her as underwater sounds, could almost certainly learn to imitate those sounds. Appropriate experiments with Phoenix or other dolphins or sea lions similarly trained to communicate by sounds might reveal whether they are capable of using acoustic signals interchangeably in both the receptive and productive modes.

## Ape Language

One of the most exciting advances in cognitive ethology was achieved by B. T. and R. A. Gardner at the University of Nevada (1969, 1971, 1984, 1989a, 1989b) when they succeeded in training a young female chimpanzee named Washoe to use more than a hundred signs derived from American Sign Language (ASL). These signs are gestures developed for communication by the deaf. Based on English, it is one of several sign languages for the deaf adapted for manual gesturing. The Gardners based their plans for this ambitious attempt to teach a gestural language to a chimpanzee on three previous investigations, among others: (1) the extensive studies of the Great Apes by R. M. and A. W. Yerkes (1925, 1929); (2) the detailed observations of natural communication between chimpanzees described by Jane Goodall (1968, 1986); and (3) the almost totally unsuccessful attempts by the Kelloggs (1933) and the Hayes (1951a, 1951b) to train chimpanzees to use spoken words, partly at least because their larynx is anatomically unsuited for producing the sounds of human speech.

Yerkes (1925, 179–80) had suggested that chimpanzees might be able to learn a gestural communication system. His and many other studies involving both laboratory experiments and the home rearing of young chimpanzees by the Kelloggs and the Hayes had abundantly demonstrated that our closest nonhuman relatives can learn numerous complex discriminations. Under natural conditions some populations of chimpanzees use simple tools, and in laboratory studies they can learn to use many human tools. Similar use of human tools by orangutans has been described in detail by Lethmate (1977). They communicate with each other by sounds and simple gestures; and captive apes, like many other birds and mammals, learn to recognize simple spoken commands. But until the Gardners' work with Washoe, chimpanzees had seemed almost totally incapable of anything even suggestive of linguistic communication. The intensive and at times heatedly controversial investigations that have followed in the footsteps of the Gardners (and Washoe) are reviewed in detail by Savage-Rumbaugh (1986) and in the volumes edited by Heltne and Marquardt (1989) and by Parker and Gibson (1990).

Washoe was acquired by the Gardners at about one year of age, and she was cared for by friendly and familiar people who communicated exclusively in American Sign Language when she was present. They signed to her about things likely to interest her, much as human parents talk to their babies. Washoe was taught simple versions of ASL signs,

partly by demonstration—use of the sign by her trainers in the presence of the object or activity for which the sign stood—and partly by molding, a procedure in which a trainer would gently hold her hands and guide them through the appropriate motions. In three years she learned to use and respond appropriately to eighty-five signs (Gardner and Gardner 1971). Subsequently several other chimpanzees and a few gorillas and orangutans have been taught to use signs derived from ASL, and vocabularies of over a hundred signs have been achieved by several of these animals, as reviewed by Ristau and Robbins (1982), and by Gardner, Gardner, and Van Cantfort (1989). Scarcely any behavioral scientists expected that Yerkes' 1925 prediction would ever be so abundantly fulfilled.

The implications of the discovery that chimpanzees and other Great Apes could communicate in even a rudimentary form of language were truly shattering to the deep-seated faith in language as a unique human attribute separating humanity from the beasts. As a result, a heated series of controversies continues to rage over the degree to which the communicative behavior learned by apes is actually a simple form of language. Many criticisms of the earlier experiments with apes have been significantly constructive, and have led to a sharpening of scientific understanding of human language and its acquisition by young children. They have also led to improved and better controlled investigations of the communicative behavior of the apes, and these in turn have served to overcome many of the criticisms of the earlier studies. On balance, it now seems clear that apes have learned to communicate simple thoughts.

Anticipating the appropriate concern that the signing apes were not really communicating linguistically, the Gardners required that quite stringent criteria be satisfied before they accepted a sign as reliably used by Washoe. It had to have been "reported by three different human observers as having occurred in an appropriate context and spontaneously (that is, with no prompting other than a [signed] question such as 'What is it?' or 'What do you want?') . . . each day over a period of 15 consecutive days" (Gardner and Gardner 1969). In later vocabulary tests, pictures of objects for which the chimpanzee had learned to ASL sign were projected on a screen visible to her but not to either of two observers who did not know what picture was shown. One observer was in the same room, and if the chimpanzee did not sign spontaneously when the picture was projected on the screen, she signed the question "What is it?" or some equivalent. The other observer watched from a separate room through a one-way glass window. Both observers noted

what sign they judged the ape to have produced, but they could not communicate or influence each other's reading of the signs until after the test was completed.

The two observers agreed in their interpretations of 86 to 96 percent of both correct and incorrect signs produced by three of four chimpanzees. The fourth animal yielded only 70 percent interobserver agreement, probably because she had not mastered signing as thoroughly as the other three. The chimpanzee's signs were correct in 71 to 88 percent of the trials, and this was far above chance levels because many signs were in use by these animals, so that if they were merely guessing at random, the expected percentage of correct signs would have ranged from 4 to 15 percent (Gardner and Gardner 1984). These "blind" tests seem to rule out the possibility that the data could have been seriously distorted by inadvertent cuing or Clever Hans errors, because neither observer could see the projection screen, and also because any such inadvertent cuing would have had to convey which of numerous signs the chimpanzee should produce in response to the projected picture.

Nevertheless some critics have pointed out that apes are very adept at detecting inadvertent cues from their human companions, and that it is conceivable that even in these blind tests the ape could have received information about which sign to produce from unintentional sounds or movements of the observers. It is also conceivable that they could have inadvertently conveyed information to each other about what sign was appropriate, as claimed by Sebeok and Rosenthal (1981) and by Umiker-Sebeok and Sebeok (1981). Although every sort of precaution and repeated checking of all possible sources of error are always appropriate, these criticisms seem quite far-fetched, and later experiments of Savage-Rumbaugh and her colleagues described below render explanations based on inadvertent cuing extremely implausible.

Washoe and other apes who have learned to use communicative gestures based on ASL seem to use these signals more or less as very young children use single words. They sign spontaneously to request simple things and activities, and they sometimes sign to themselves when alone. Washoe and other signing chimpanzees sign to each other to at least a limited extent (Fouts 1989; Fouts and Fouts 1989; Fouts, Fouts, and Schoenfeld 1984). A three-year-old chimpanzee named Ally was trained by the Gardners' methods to use about seventy signs, and he also learned to understand several spoken words and phrases. Next he was taught to use new signs corresponding to ten of these words that referred to familiar objects, but only the signs and not the objects themselves were presented along with these spoken words during this phase

of the training. After this was accomplished, Ally was shown the objects and he identified them by means of the signs he had learned from their spoken names (Fouts, Chown, and Goodman 1976). Signing chimpanzees sometimes transfer signs to new situations, different from those in which they had been trained to use them. For instance, Washoe learned the sign for "open" to ask that doors be opened, but she then used it to request her human companions to open boxes, drawers, briefcases, or picture books, and to turn on a water faucet. After she had learned the sign for flower, she used it not only for different kinds of flowers but also for pipe tobacco and kitchen fumes. To her, it evidently meant smells.

Stimulated by the Gardners' success with Washoe, other investigators have achieved similar levels of communication not only by several other chimpanzees but also by gorillas (Patterson and Linden 1981) and an orangutan (Miles 1990). Still other investigators have studied the communicative abilities of apes by quite different procedures. Premack and his colleagues concentrated on a type of symbolism based on plastic tokens, which chimpanzees learned to arrange on a sort of bulletin board in order to request desired objects and answer simple questions about them. These plastic symbols were arbitrary in that they did not resemble the object for which they stood. Premack's star pupil, Sarah, learned not only to select the correct symbol when shown the object for which it stood, but to use the symbols to request things she wanted. She could also arrange plastic tokens in strings resembling rudimentary sentences, and answer simple questions presented to her through similar arrangements of the tokens. She could answer such questions as "What is the color of ——?" about the plastic representations of objects, even when the colors and other properties of the tokens were quite different from those of the objects for which they stood (Premack 1976, 1983b; Premack and Premack 1983).

In another ambitious project Rumbaugh, Savage-Rumbaugh, and their colleagues at the Yerkes Laboratory in Atlanta, Georgia, use a keyboard connected to a computer that records which keys are activated by either a human experimenter or the ape that learns which key it must touch to obtain specific objects or to express simple desires. Each key lights up when pressed, and each has a characteristic pattern to help the apes recognize and select it; but these patterns are not iconic representations of the objects for which the key stands. This system permits two-way communication; and it has the great advantage that an objective record can be kept of every key press.

The initial experiments with plastic tokens and keyboards were inter-



preted as showing that the chimpanzees were using a simple type of linguistic communication, including a rudimentary sort of grammar in which the tokens or key presses were used in a specific sequence to express relationships between the individual symbols. But, as reviewed by Savage-Rumbaugh (1986), these apes may have learned only to perform specific actions to obtain particular things or activities. They may have been thinking something like "If I do this, he will give me some candy," or "If I do that, she will play with me." They seldom, if ever, tried to use their newly acquired skills to initiate communication with their human companions or with each other, partly because the experimental arrangements in these early investigations allowed rather little opportunity for such spontaneity. On the other hand, Washoe and other apes taught to communicate by manual gestures did often initiate communicative exchanges by spontaneously asking for things they wanted.

All these approaches to teaching language-like communication to chimpanzees have been successful in the general sense that the apes have learned to make requests and to answer simple questions. They have also learned to give the appropriate gestural sign, to press the correct key, or to select the right plastic symbols to label familiar objects. Serious theoretical questions have been raised, however, about the degree to which such apparent communication entails any true understanding on the animal's part of the meanings of the signals and symbols. The alternative interpretation that has been suggested by many critics is that the chimpanzee learns merely to perform certain actions in order to obtain things it wants, including activities or actions on the part of the human companions, such as opening doors or going for a walk. These distinctions, and the evidence that indicates the degree to which the language-trained apes understand what they are communicating, will be discussed in more detail below in relation to the recent studies of Savage-Rumbaugh and her colleagues.

First it is appropriate to consider a fundamentally important aspect of human language and the evidence for its presence or absence in the language-like behavior learned by Washoe and her successors. This is what the psychologist George Miller (1967) has aptly termed "combinatorial productivity." Human speech combines units in various ways to give new meanings not expressed by the units themselves, typically by the use of grammatical rules common to all users of a given language. A simple example is the use of word order in English and few other languages to indicate which word designates the actor and the object of the action ("John hits ball" versus "Ball hits John"). In most languages many of these relationships are conveyed by modifications or inflections

of the words, rather than by word order. But regardless of how it is done, rule-governed combinations of words convey a much wider array of meanings than would be possible if each word were entirely independent, and its relationship to other words did not convey any additional meaning. Such grammatical or syntactical rules are so important in making possible the richness and versatility of human languages that linguists and many others often maintain that syntax is a *sine qua non* of language, and that the use of words or their equivalent is not sufficient to qualify as true language. This view must of course entail denial of true language to young children with vocabularies of only a few words.

The importance assigned to syntax led to great interest in the combinations of signs used by Washoe and other signing apes, and to efforts by Premack and his colleagues as well as the scientists at the Yerkes Laboratory to determine to what extent chimpanzees could communicate syntactically. Terrace (1979) replicated the Gardners' training of a young chimpanzee to use signs derived from American Sign Language, and he devoted special attention to series or combinations of signs used by this animal, named Nim Chimpsky. The results were disappointing. A few combinations of two or three signs were used, but only to a very limited extent did Nim attain anything like the combinatorial productivity of human language. When two or more signs were used, there was little consistency in their order, and in only a few cases was sign combination AB used differently from BA. Most series of signs were repetitious, with third or later signs adding almost nothing to the message conveyed. Furthermore, many of Nim's signs were repetitions of the immediately preceding signs of his human companions.

Terrace (1979) and Terrace, Petitto, and Bever (1979) report that one of the longer series of signs used by Nim was "Give, orange, me, give, eat, orange, give, me, eat, orange, give, me, you." And one of the longest utterances reported by Patterson and Linden (1981) from the gorilla Koko was "Please milk, please, me, like, drink, apple, bottle." Terrace and others have concluded that signing apes are not using anything that deserves to be called a language, because of the almost total lack of rule-governed combinations of signs. But however ungrammatical and repetitious these strings of signs may have been, they leave no doubt what Koko and Nim wanted. Terrace's findings have had a widespread and negative impact, causing many to dismiss the whole effort to teach language-like communication to apes as unimpressive and insignificant. But this dismissal is based on the absence or near absence of combinatorial productivity, and it does not seriously detract from the significance of signing, as evidence of what apes are thinking.

The reasons advanced for denying that the signing of apes serves a function equivalent to human language have included the argument that many of the signs adapted from ASL are similar to naturally occurring communicative gestures (Seidenberg and Petitto 1979). This seems to a biologist quite the opposite of a reason for denying a language-like function. Perhaps chimpanzees have already developed their own types of gestural communication, more versatile than anything ethologists have yet deciphered, and the training achieved by the Gardners and their successors has simply elaborated on an ability already present. If so, gestural communication is more than an artifact of human training; it may well be a part of the natural behavior of the Great Apes. Seidenberg and Petitto (1979, 199) seem to believe that natural gestures of chimpanzees are unlearned, and therefore different from and inherently inferior to human language. But Jane Goodall's descriptions of chimpanzee society show abundant opportunity for young animals to learn communicative behavior from their older companions. Washoe and other signing apes may not have, literally, learned ASL; but their signing nevertheless conveys some of their thoughts.

Words are obviously basic to any sort of linguistic communication. Without grammar or combinatorial productivity, words are limited and clumsy; but they do suffice to communicate thoughts. Grammar adds greatly to the economy and versatility of human languages, to its refinement and scope, but grammar without words would be empty and useless. Without adhering to his dualistic philosophical view that animals are incapable of any sort of rational thinking, one can agree with Descartes, as paraphrased by Chomsky (1966), that "*the word is the sole sign and certain mark of the presence of thought.*" Descartes and Chomsky claim that nonhuman animals are incapable of using anything equivalent to words, so that the key question is whether the signs used by signing apes have the essential properties of words.

Savage-Rumbaugh (1986, 15–32) has clarified these questions by emphasizing that much of the early testing of language-like communication of apes did not suffice to show that their communicative behavior was fully equivalent to human use of words, even those used by young children with limited vocabularies. She agrees with Nelson (1977) and other students of language acquisition by human children that "the essence of human language is not found in syntax" but (quoting Nelson) in "the translation of meanings and the expression of these meanings to a social partner for some functional purpose . . . (and) the interpretation of the meaning expressed by others." Thus to qualify as a true

word, a communicative signal must convey meaningful knowledge, and its user must be able to employ it both to transmit and to receive such knowledge. According to this definition, the ability to produce the correct sign when shown the object for which it stands is not enough; to serve as the equivalent of a word the sign must also be used on appropriate occasions to convey some sort of knowledge. This leads to the question of naming. Savage-Rumbaugh points out that producing the correct signal when shown an object does not necessarily correspond to human naming of the object. Only if the ape (or other animal) also uses the signal spontaneously to designate an object that is not actually present, and thus cannot be a direct stimulus to the signaling behavior, can one conclude that the animal is naming something.

To qualify as the equivalent of a word, Savage-Rumbaugh believes, a communicative signal must have the following four attributes: (1) it must be an arbitrary symbol that stands for some object, activity, or relationship; (2) it must convey stored knowledge; (3) it must be used intentionally to convey this knowledge; and (4) recipients must be able to decode and respond appropriately to the symbols. If we leave aside for the moment the stipulation that communication be intentional (which is of course anathema to inclusive behaviorists, but which I will discuss below in relation to Grice's criteria for linguistic communication), many types of naturally occurring animal communication satisfy these criteria, at least in general terms. For example the honeybee waggle dances include an arbitrary symbolism conveying direction relative to an invisible sun or pattern of polarization of the blue sky; this knowledge has been stored by the forager, and recipients decode the symbols and react appropriately. But Savage-Rumbaugh points out that many of the vocabulary tests reported for Washoe and other signing apes (and also for dolphins and sea lions) were limited to demonstrating what linguists call receptive competence, the ability to understand, or at least to react appropriately to a particular communicative signal.

Savage-Rumbaugh argues that only when the ape also uses the symbol to convey to others something they did not already know does it begin to serve as something like a word. The waggle dances of honeybees convey to other bees important information they did not have previously. Signing apes ordinarily begin to use a symbol as some sort of request; they learn to use ASL signs, plastic tokens, or keys on a keyboard to manipulate the behavior of their companions. This is one type of what linguists call productive, as opposed to receptive, communication. Again, most natural animal communication includes both produc-

tive and receptive use of communicative signals, but many experimental tests of language-like behavior learned by animals have been limited primarily to one of these two fundamental attributes.

Another sort of objection against equating the performance of the signing apes with human language has been raised by philosophers such as Grice (1957) and Bennett (1964, 1976, 1988, 1991). The former argued that for true language use a speaker must intend to communicate to a listener, and that the speaker must intend to induce a belief, or a change in belief, in an audience, and must also intend that the communication be recognized by the audience as having such intent. Bennett suggests that apes such as Washoe use signs as injunctions, requests, commands, and the like, whose purpose is to produce a desired behavior on the part of the recipient rather than trying to change the recipient's beliefs, as Bennett believes most human language users seek to do. It is difficult enough to gather even suggestive evidence about the beliefs of nonhuman animals, and it is doubly difficult to obtain any hints as to whether they try to change beliefs as well as behavior of others. These more philosophical questions about just what animals intend to achieve by their communicative behavior must remain open until better methods are developed to learn more about just what, if anything, they are consciously thinking.

Still another feature of human language that is generally believed to be lacking in all animal communication systems, including those of the signing apes, is creativity, that is, the ability to conceive and convey new messages, different from anything ever thought or said before. It is often claimed that an animal's communication is limited to a few relatively fixed signals that are genetically determined, and that it is incapable of producing novel communicative signals in newly arisen circumstances. Not all animal signals are rigid and invariant; in fact, one contrast with human language that is often emphasized is the graded nature of many animal signals that are believed to be expressions of emotion varying only in intensity but lacking any semantic content. As mentioned above, a few clear exceptions to this generalization are now known, such as the semantic alarm calls of vervet monkeys analyzed by Seyfarth and his colleagues (1980).

If animals did spontaneously produce novel signals, these would be difficult to detect because they would probably seem to be meaningless variations of known signals. Some signs do seem to have been "invented" by Washoe and other signing apes, but it is very difficult to be sure that no precursors were included in the rich variety of signing and other social interactions with human caretakers and trainers. We have

one clear example of complex animal signals that change over time in the songs of male humpback whales, which undergo gradual changes from season to season (Payne and Payne 1985). But it unfortunately is not yet clear what messages these songs actually convey, so that there is no way to tell whether they constitute new or altered signals, or changes in the acoustic features conveying the same basic message.

Savage-Rumbaugh and her colleagues at the Yerkes Laboratory have improved upon the earlier studies of language-like behavior in apes in several important ways, as described in her recent monograph dedicated to Sherman and Austin, two of her star subjects (Savage-Rumbaugh 1986). They are male chimpanzees who learned to use tools to open containers from which they could obtain desired foods, as other Great Apes have done (for examples see Lethmate 1977). But Sherman and Austin also learned to use the Yerkes keyboard system to ask each other to pass the needed tool through a small window. Previously they had learned to request desired foods, but they required much additional training before moving on to what for chimpanzees is apparently a more difficult task, namely, learning to use the keyboard both to transmit and to receive information. Much ingenious experimentation was required to teach them to use the keyboard for this type of cooperative communication; but at many points in the long and complex series of attempts, both Sherman and Austin seemed suddenly to grasp what they had to do and then proceeded to learn new applications of the same basic type of communicative behavior rapidly and with relatively few errors.

As one reads Savage-Rumbaugh's detailed and meticulous account of the gradual acquisition by Sherman and Austin of the ability to request the appropriate tool needed to obtain food from a particular type of container, it becomes evident that these animals gradually "caught on" to this novel and complex task, and that once they understood what to do, they proceeded with enthusiasm to apply their new skill. Blind tests of their abilities included situations in which Austin watched a teacher place food in a type of container from which it could be removed only by using a particular tool. For example, the food might be placed in the middle of a long, transparent, horizontal tube from which it could be removed by poking with a long thin stick. The teacher then moved out of the room, and Austin went to a keyboard inside the room and requested the stick by pressing the appropriate key. The keyboard was some distance from the food container, and by the time the keyboard was turned on, the teacher was out of Austin's sight and hence unable to provide even inadvertent cues as to which key he should press.

Six tools were available outside the room: a key used to open various locks, coins that operated a vending machine, straws to obtain liquids through small holes, long sticks needed to push food out from the middle of the horizontal tube, sponges to soak up liquids from vertical tubes, and a socket wrench to open various bolted doors. Both Sherman and Austin had used all these tools extensively to obtain desired foods, but in these tests they had to obtain them by pressing the appropriate key while alone in the room, then walk outside to the tray of tools. Here the teacher was equipped with a projector that displayed which key the ape had pressed while still alone inside the room, and if it was the correct one, he was given the requested tool and could carry it back to the baited container and use it to get the food that was otherwise inaccessible. These tests ruled out inadvertent cuing even more convincingly than earlier experiments by the Gardners and others.

After Sherman and Austin had learned to communicate about tools, the situation was gradually changed so that in order to obtain the food, one of them had to request that the other give him the appropriate tool. The two were located in adjacent rooms, but they could see each other through a window equipped with a small opening through which tools or pieces of food could be passed back and forth. Since Yerkes Laboratory keyboards were located conveniently beside each window, Sherman and Austin could communicate by pressing the keys while watching each other through the window. When the keyboard system was turned on, touching a key caused it to be back lighted, so that both chimpanzees and the experimenters could see which key had in fact been activated. In some experiments there was also a large replica of the keyboard on a wall of the room, enabling all concerned to see which key had been pressed. At the start of each experimental session the window was covered, and food was placed in one of several types of closed containers. This was clearly visible to the chimpanzee in that room, but the tools necessary to open the container were located in the other room. When the cover was removed from the window, the first chimpanzee used his keyboard to ask the other to provide the type of tool needed to open the particular container in which the food had been placed. After the correct tool was passed through the small opening in the window, the first chimpanzee opened the container and passed at least some of the food to the animal in the adjacent room who had provided the necessary tool.

It took a considerable amount of training to teach these procedures to Austin and Sherman, especially the sharing of food; but once they had learned how to engage in this cooperative communication, they

repeatedly and efficiently followed these procedures to obtain desired foods. They both became adept at playing both roles. If the keyboard was turned off so that no keys were illuminated, the appropriate tool was handed over only at about a chance level, indicating strongly that the keyboard communication was necessary, and that no other unrecognized form of information transfer would suffice. During the first five days when such cooperative communication about tools was called for, the percentage of correct signs rose from 77 percent correct for Sherman and 91 percent for Austin out of forty-seven trials on the first day to 91 percent for Sherman and 97 percent correct for Austin out of ninety trials on the fourth and fifth days combined. Somewhat more errors were in requests than in the tools provided, but the whole process was remarkably effective. On the sixth day the keyboards were turned off so that the second ape could not see which key his companion had pressed, and the proportion of correct scores fell to 10 percent.

Many additional indications that this cooperative communication was fully intentional were provided by the behavior of Sherman and Austin when requests for a tool did not lead to an appropriate response. The first chimpanzee then often gestured vigorously, tried to orient his companion's attention to the keyboard, and pressed the requesting key repeatedly and emphatically. Savage-Rumbaugh (1986) provides detailed descriptions of the many complex ways in which Sherman and Austin interacted while communicating and sharing food, and the apparent game playing in which they often indulged. These accounts make it abundantly clear that these two apes were intentionally communicating by means of the Yerkes keyboard as well as by gesturing, and that they not only understood but often enjoyed what they were doing.

Until the 1980s, language-like behavior had been studied primarily in common chimpanzees (*Pan troglodytes*) with a few studies also showing that similar signing behavior can be learned by gorillas and orangutans. But there is another species of the genus *Pan*, the pigmy chimpanzee or bonobo, *Pan paniscus*. One of the two chimpanzees first studied in detail by Yerkes was a bonobo, and while they are less commonly available in captivity, bonobos are clearly more versatile than common chimpanzees. A male bonobo named Kanzi, born at the Yerkes Laboratory, has demonstrated much greater communicative spontaneity than Sherman and Austin or other common chimpanzees, as described by Savage-Rumbaugh (1986) and Savage-Rumbaugh and her associates (1989). As a dependent youngster, beginning when he was six months old, Kanzi accompanied his mother during prolonged efforts to teach



her to use the Yerkes keyboard, but no effort was made to teach him which keys had which meanings, or indeed to use the keyboard at all. But the trainers used gestures and spoken English to communicate with him, and he had abundant opportunity to observe how the keyboard was used for communication by his human companions, and to a limited extent by his mother.

Beginning at about eighteen months, Kanzi spontaneously began to use gestures such as pointing in directions he wished to be carried, or making twisting motions toward containers when he needed assistance in opening their lids. When he was two and a half years old his mother was withdrawn from the training, partly because she was making very little progress. At that time Kanzi began using the keyboard to request desired objects and even to communicate about things that were not present, such as desired foods or locations to which he wished to travel. This took place without any specific training; evidently he had discovered for himself how the keyboard operated by watching the human trainers use it, and also perhaps by watching their relatively unsuccessful efforts to teach its use to his mother. By the time he was forty-six months old, Kanzi was using at least eighty keys more or less as words. A symbol was "classified as a member of Kanzi's vocabulary if and only if it occurred spontaneously on 9 of 10 consecutive occasions in the appropriate context *and* was followed by a behavioral demonstration of knowledge of the referent. For example, if Kanzi requested a trip to the 'treehouse' he would be told, 'Yes, we can go to the treehouse.' However, only if he then led the experimenter to this location would a correct behavioral concordance be scored" (Savage-Rumbaugh 1986, 389).

Kanzi's use of the keyboard is much more spontaneous than the signing performed by Nim, which led Terrace and others to conclude that such signing had little in common with human language. The majority of Kanzi's "utterances" via the keyboard are not imitations of key presses by his human companions. He also uses many more, and longer, combinations of key presses than Nim exhibited with his signing, although Savage-Rumbaugh does not feel that these are rule-governed like human grammar. But to a much greater extent than with Nim, the individual "words" add meaning to previous members of a string of key presses. Kanzi also uses many gestures, which add meaning to the "words" he produces by key presses. In well-controlled blind tests in which the experimenters cannot see pictures shown to Kanzi, he presses the corresponding key. He can also do this in response to spoken words.

Recent studies presented in detail by Greenfield and Savage-

Rumbaugh (1990) have demonstrated that, unlike Nim in Terrace's earlier studies, Kanzi learned to use simple grammatical rules in his communication with his human companions. He used these rules productively and he also comprehended their use by others. He even invented a few of his own rules. Kanzi's accomplishments thus call into serious question the generalization that only human language employs meaningful rule-governed combinations of individual communicative elements. Furthermore, his invention of simple but meaningful combinations suggests combinatorial productivity, a property that had previously appeared to be limited to human language, as emphasized by Miller (1967).

In short, Kanzi, and to a lesser extent other bonobos at the Yerkes Laboratory, have learned to use a combination of gestures and the Yerkes keyboard to achieve fluent two-way communication with their human companions. The versatility and spontaneity with which Kanzi does this, together with the behavioral concordance between what he asks for and what he does subsequently, make it abundantly clear that he can voluntarily communicate simple desires and intentions. His communication certainly serves as an effective "window" on what he is feeling and thinking. The richness and versatility of both his communication and the thoughts it conveys is greater than that displayed by other animals, even by other Great Apes.

The obvious significance of these discoveries about the acquisition of language-like communicative abilities in the Great Apes should be viewed against a background of many other demonstrations that these animals possess superior mental capabilities. A thorough review of primate intelligence is far beyond the scope of this book, but two recent discoveries are especially significant. Boesch (1991) has observed that occasionally mother chimpanzees actively demonstrate to their young how to open hard nuts by the use of stone tools. This appears to be a simple case of intentional instruction, despite the widespread belief that teaching is a uniquely human ability. De Waal (1990) has recently analyzed an intriguing behavior pattern in which rhesus macaque mothers hold their own infant together with another of roughly the same age. In most cases the other infant is the offspring of a dominant female. It seems likely that this behavior increases the likelihood that her infant will later benefit by association with more dominant companions, and that these monkeys are intentionally attempting to "promote future associations between their own offspring and high-ranking youngsters."

These many discoveries about the mental and communicative skills of both dolphins and apes demonstrate brilliantly how cognitive ethol-

ogy can progress by careful and critical observations and experiments. They also confirm that the Gardners were quite correct in their earlier conclusions based on experiments with Washoe and other signing chimpanzees. The original experiments have been greatly improved upon, and more conclusive blind tests and other procedures have answered the many criticisms advanced to avoid the conclusion, that seems so unpalatable to many behavioral scientists and others, that apes can use the equivalent of words to communicate a rich array of feelings and thoughts. Human language and thought may be, in the words of Donald (1991,136), "light-years removed from Kanzi's accomplishments." But the ape language experiments have clearly demonstrated evolutionary continuity between human and nonhuman communication and thinking.

## *The Significance of Animal Consciousness*

**T**hree basic and interrelated reasons for our concern with animal mentality stand out as especially significant. For convenience they may be designated as *philosophical*, *ethical*, and *scientific*. This chapter will briefly review why they are important and suggest how our current ignorance about them can be reduced. The philosophical importance of animal consciousness lies in its relevance to the general question of other minds and to the difficult questions of how to define and identify consciousness. The ethical importance lies in the widespread belief that causing pain and suffering to a conscious creature is morally wrong in an important sense not applicable to an unfeeling mechanism. And the scientific importance lies in our interest in animals as such. We want to understand what the lives of these other creatures are like, to them.

Previous chapters have discussed several kinds of animal behavior that suggest conscious thinking, especially cases in which animals communicate messages that are probably expressions of simple thoughts. These examples have been selected primarily because evidence is available about the animal's previous experience and the versatility of its behavior as it adjusts to challenges that would seem difficult if not impossible to predict. The ability to handle unpredictable, or barely predictable, situations makes it unlikely that either evolutionary selection or learning from previous experience could provide a specific prescription for what the animal should do. If members of a particular species are capable of perceptual consciousness (Natsoulas' Consciousness 3, defined in chapter 1) under some conditions, it seems likely that they make use of this ability under many circumstances where it is useful. And it is obvious that thinking about the probable outcome of various possible actions would be very useful in a wide variety of situations where animals must make choices that have important effects on their survival and reproduction. Thus the cases where suggestive evidence of

conscious thinking has become available could well be the tip of a large figurative iceberg.

But does it really matter whether any animals are ever conscious, and, if any are, which ones and under what conditions? Strict behaviorists tend to argue that it doesn't matter, thereby impaling themselves on the horns of a dilemma. Either they must deny the importance of human consciousness, or they must accept its importance but hold that no other species can be conscious to a significant degree. A conscious organism is clearly different in an important way from one that lacks any subjective mental experiences. The former thinks and feels to a greater or lesser degree, while the latter is limited to existing and reacting. One important difference between unconscious and conscious thought is that the latter includes paying attention to internal images or representations, that is, thinking about them to oneself. Such representations may involve any sensory modalities; they may be directly elicited by contemporary external stimulation, they may be based on memories, or they may be anticipations of future events. They can also be literal imagination of objects and events that do not actually exist.

Many behaviorists claim that the distinction between conscious and unconscious mental states is an empty and meaningless one, at least when applied to nonhuman animals, because, they say, anything an animal does might equally well be done without any accompanying consciousness. In one sense this is simply a denial of concern, a confession of limited interests. But it is often combined with an appeal to scientific parsimony and an insistence that consciousness is a needless complication, and furthermore that it does not matter whether animals, or even people, are conscious of anything at all. This attitude often leads to such sweeping and dogmatically negative pronouncements as: "The idea that people are autonomous and possess within them the power and the reasons for making decisions has no place in behavior theory" (Schwartz and Lacey, 1982, 16).

Inclusive behaviorists see no way to determine what thoughts or feelings, if any, are experienced by a member of another species. Philosophical purists of the school known as skeptics make essentially the same argument about our conspecifics. Perhaps the most appropriate response to both these claims is to point out that total perfection of argument and proof is seldom available in science any more than in general affairs. We can only make stronger or weaker claims with a higher or lower probability of correctness. Even when vital practical decisions are at stake, we have no choice but to act on whatever interpretation appears most likely to be correct, based on the most balanced assessment

of available evidence of which we are capable. We do not know whether conscious mental experiences are correlated with any specific and identifiable states or activities of central nervous systems, although of course certain parts of the human brain such as Wernicke's area are clearly of great importance. But this ignorance of ours does not mean that conscious experience is nonexistent.

Midgley (1983) and Radner and Radner (1989) have lucidly exposed the limitations and inconsistencies of behavioristic denigration of animal consciousness. Midgley emphasizes the overwhelming advantages provided for understanding animal behavior by the assumption that animals experience simple feelings, fears, desires, beliefs, and the like. A literal adherence to the behavioristic prohibition against consideration of any subjective mental experiences tends to render much animal behavior unintelligible. Humphrey (1980, 60) has forcefully made a similar point with respect to social animals:

Academic psychologists have been attempting by the "objective" methods of the physical sciences, to acquire precisely the kind of knowledge of behaviour which every social animal must have in order to survive . . . [but] they have been held up again and again by their failure to develop a sufficiently rich or relevant framework of ideas. . . . Indeed, I venture to suggest that if a rat's knowledge of the behaviour of other rats were to be limited to everything which behaviourists have discovered about rats to date, the rat would show so little understanding of its fellows that it would bungle disastrously every social interaction it engaged in.

As mentioned in chapter 1, a helpful analogy can be drawn with the history of genetics. The reality of heredity has always been obvious, but the biological mechanisms by which offspring come to resemble their ancestors to some degree, though of course not completely, has been largely explained during the past century by a series of interrelated biological discoveries of gametes, chromosomes, genes, DNA, and RNA. The gene was originally a theoretical construct based on inferences from the results of experiments such as those that demonstrated unitary inheritance of some (but not all) characters, and linkage that permitted the inference of chromosomal crossing over. Only much later were genes found to consist of DNA and RNA. Before the mid-twentieth century, geneticists did not know what genes actually were, although they had good reason to infer that they must exist within chromosomes. Had the study of heredity been impeded by taboos comparable to those that discourage students of animal behavior from investigating animal mentality, the progress of genetics would have been seriously and need-

lessly impeded. To be sure, geneticists could gather relevant empirical data from breeding experiments, while behaviorists deny that any objectively verifiable data about mental experience can ever be obtained. But the evidence from expressive communication and from versatility of behavior that has been reviewed in previous chapters is certainly suggestive, and with further refinement could well lead to adequately objective data on which inferences about the mental experiences of animals can be based.

### Philosophical Issues

Many philosophers have wrestled with the question of how we can know anything about the minds of others, whether they be other people, animals, extraterrestrial creatures, or artifacts such as computer systems. Some are convinced that other minds are found only in our species, while others consider it possible, or even likely, that they can also be found in animals or computers. Philosophers struggle to devise logical and reasonable criteria for the presence of minds and consciousness, criteria that can be applied to animals or to computer systems as well as to borderline human cases such as newborn infants or persons with severe brain damage. When many of these criteria were first proposed they seemed to be impossible for any nonhuman animal to satisfy. But, as emphasized in previous chapters, increasing understanding of animals and their behavior has often disclosed cases where the criterion in question is satisfied after all.

A few philosophers have been deeply concerned with the possibility that animals have minds of some sort, and have tried to infer what their thoughts and feelings are likely to be. Most of these inferences have been based on rather casual observations of dogs and cats, or squirrels in a city park. But recently a few philosophers have taken the trouble to inform themselves about what a wider variety of animals do under natural conditions or in laboratory experiments. For example Dennett (1983, 1987, 1988) visited the Seyfarths at their study area in East Africa to see how they observe and analyze the semantic communication of vervet monkeys, as discussed in chapter 8. This has led to a stimulating and helpful exchange of ideas concerning the degree of intentionality displayed by these monkeys in their communication about predators, even though Dennett (1989) has more recently described the inquiry into possible animal consciousness as a wild goose chase.

Sober (1983) has lucidly analyzed the limitations of behaviorism and the problems that have discouraged psychologists and others from de-

voting much attention to mentalism, that is, to investigation of those inner states such as beliefs, desires, intentions and the like appear to influence behavior. He points out that many of the behaviorists' objections to mentalism can be applied with equal force to behaviorism itself. For example, the claim that mentalism is "too easy" because one can always dream up some hypothetical mental state to explain any behavior can be countered by pointing out that when behaviorists claim that whatever a person does must have resulted from prior conditioning, they are often stating an assumption about such causation rather than being able to identify in any plausible fashion just how the person was conditioned to do what he does. Thus the argument that statements about mental states cannot be verified or falsified can be applied with equal force to many behavioristic explanations. Sober also points out that just because the beliefs or other mental states of animals cannot have as rich a content as their human counterparts is no reason to deny their existence or significance.

Lycan (1987) has discussed the philosophical issues surrounding the nature of consciousness from the viewpoint of a "teleological functionalist" who recognizes the likelihood that mental experiences constitute an evolutionary continuity like other biological characters. He considers mental experiences to have the property of intentionality, used in the philosopher's sense of "aboutness," that is, they relate to something, real or imagined. He holds "that to be in an intentional state is to host a mental representation, a brain state that bears a natural (causal and teleological) relation to the object represented or, in the case of abstract or nonexistent objects, to linguistic events that go proxy for them" (Lycan, 1987, 71). This definition is quite applicable to mental representations of animals, especially if we extend the customary idea of linguistic events to include events described by animal communication.

Thomas Nagel (1974) stimulated the interest of many philosophers in such questions by inquiring what it is like to be a bat. He concluded that because bats are so different from us, and especially because they rely so heavily on echolocation, we can never know precisely what life is like to an insect-eating, sonar-guided flying mammal. But Nagel does not deny that partial understanding and significant, though incomplete, information about the experiences of bats or other animals can be deduced from their behavior. While he may be quite correct that we cannot hope for perfect, total descriptions, we can make substantial progress, and informed inferences about animal thoughts can eventually come to be as well grounded as the conclusions reached in many other areas of biological inquiry.



Specifically in the case of bats specialized for echolocation, we can base some preliminary estimates on the inadequately recognized similarity between the echolocation of bats and the detection of obstacles by the human blind by means of sounds and echoes. Blind people, and blindfolded volunteers who have had considerable practice, can detect and classify objects in their vicinity by emitting audible sounds and hearing subtle differences depending on the presence of the object. But, curiously enough, many of the most proficient do not consciously recognize that they are accomplishing this by the sense of hearing. Instead they report that they simply feel that something is out there, and a common term for this ability is “facial vision” (Griffin 1958; Rice 1967a, 1967b). Nevertheless the feeling and the alleged “vision” cease almost totally if they can make no sounds or if their hearing is blocked. We might guess that when bats detect and identify insects by echolocation they perceive not a special pattern of echoes but rather the presence, position, and location of an object with certain properties—such as an edible insect or a falling leaf. Thus it may not matter very much for an animal’s perceptual consciousness whether the sensory information on which perception is based is visual, auditory, or even a modality even more remote from our experience, such as the electric sensing of weakly electric fishes.

The philosopher John Searle (1983, 1984, 1990b) has analyzed the cogent reasons for recognizing that conscious thinking is of the greatest significance. Although he discusses primarily human consciousness, several of his arguments are equally applicable to animals. For example, after explaining the philosopher’s definition of intentionality as “that feature of certain mental states or events that consists in their . . . being directed at, being about, being of, or representing certain other entities and states of affairs,” he writes: “Consider the case of an animal, say a lion, moving in an erratic path through tall grass. The behavior of the lion is explicable by saying that it is stalking a wildebeest, its prey. The stalking behavior is caused by a set of intentional states: it is *hungry*, it *wants* to eat the wildebeest, it *intends* to follow the wildebeest with the *aim* of catching, killing, and eating it” (Searle 1984, 14–15).

After emphasizing that the rejection of teleology by seventeenth-century physics, and the nineteenth-century Darwinian account of the origin of species, were “liberating steps,” Searle comments: “But ironically the liberating move of the past has become constraining and counterproductive in the present. Why? Because it is just a plain fact about human beings that they do have desires, goals, intentions, purposes, aims, and plans, and these play a causal role in the production of their

behavior. Those human sciences in which these facts are simply taken for granted, such as economics, have made much greater progress than those branches, such as behavioristic psychology, which have been based on an attempted denial of these facts. Just as it was bad science to treat systems that lack intentionality as if they had it, so it is equally bad science to treat systems that have intrinsic intentionality as if they lack it" (Searle 1984, 15).

More recently, Searle (1990, 585) states that ten years ago he thought

the major mistake we were making in cognitive science was to think that the mind is a computer program implemented in the hardware of the brain. I now believe the underlying mistake is much deeper. We have neglected the centrality of consciousness to the study of mind. . . . If you come to cognitive science, psychology, or the philosophy of mind with an innocent eye, the first thing that strikes you is how little serious attention is paid to consciousness. Few people in cognitive science think that the study of the mind is essentially or in large part a matter of studying conscious phenomena: consciousness is rather a "problem," a difficulty that functionalist or computationalist theories must somehow deal with. . . . As recently as a few years ago, if one raised the subject of consciousness in cognitive science discussions, it was generally regarded as a form of bad taste, and graduate students, who are always attuned to the social mores of their disciplines, would roll their eyes at the ceiling and assume expressions of mild disgust.

### Thoughtless Brutes?

In a presidential address to the American Philosophical Association, Malcolm (1973) expressed his dismay at the idea that dogs, or presumably other animals, might experience thoughts that they could not express for lack of language. "The relationship between language and thought," he continued, "must be so close that it is really senseless to conjecture that people may *not* have thoughts, and also really senseless to conjecture that animals *may* have thoughts." But others have dissented from such a necessary linkage between language and thinking. For example, Ferguson (1977) emphasized the important role of pictorial thinking in technology. And MacNamara (1977, 2) argued that "my knowledge of the world is in the form of representations whose function as representations does not depend on any resemblance between themselves and the objects represented." Thus, as discussed in detail by Alport (1983), many scholars have abandoned the formerly

widespread belief that human language is essential for conscious thinking.

In recent years other philosophers have taken a new interest in animal mentality, and some have expressed an updated version of Malcolm's general view. For example, the neurophysiologist Eccles debated these basic issues with Wade Savage in a book edited by Globus, Maxwell, and Savodnik (1976). Eccles (p. 159) argued that "in the biological world only human beings are endowed with a self-consciousness, and with a cultural creativity, and they are distinguished completely from animals by the ability to think logically, creatively, and imaginatively and to communicate these thoughts in every medium of cultural expression." Wade Savage countered (p. 152) with the opinion that "animals, too, have souls: feelings, desires, purposes, thoughts, consciousness, rights—the same rights to life and to the absence of pain that we accord to humans . . . refusal to make this concession seems, to this author, to be the product of human vanity." In this context Wade Savage seems to mean by the word soul something close to conscious mental states rather than anything necessarily immaterial or spiritual.

Johnson (1988, 282, 288) has recently argued that most animals are incapable of believing something, except possibly for the Great Apes. He agrees with Armstrong (1973) that animals perceive and that their perceptions affect their behavior, but he differs from Armstrong in holding that something more is necessary to qualify as a belief. This additional requirement, Johnson argues, includes a causal role for a true belief in affecting behavior, although it is difficult to see that this distinction is fundamental since he recognizes that perceptions influence an animal's behavior. He supports his position by claiming that animal behavior is determined by "internal processes very different from those humans employ." This view tends to reinforce the widespread assumption that human mental experiences are the only kind that can exist. But another interpretation is that Johnson and others are coming to recognize that animals probably do experience simple conscious thoughts, although human thoughts are held to be the only ones worthy of serious consideration. In this vein Johnson asserts as self-evident that "flies do not reason on the basis of meanings or goals, but simply react automatically to cues." He also claims that animal thinking "takes no account of meanings," but gives no reasons for excluding, for example, the possibility that when an animal sees a distant predator this means that appropriate escape behavior is called for. He seems to take it for granted that only our species is capable of internal processes qualifying as beliefs, so that his arguments are little more than reiteration of a prior conviction.

Here we see a philosopher basing his arguments about other minds on opinions about animal behavior, in particular the widespread conviction that all insect behavior is rigidly stereotyped. The goals of insects may be simple compared to the theories of philosophers, but we have no firm basis for dogmatically ruling out conscious perception of simple meanings and desired goals, such as a honeybee's waggle dance meaning food is located at a certain distance and in a certain direction, or the goal of escaping a predator by running to a safe shelter. Johnson goes on to offer as evidence against the presence of beliefs the fact that birds can be fooled when several hunters enter a blind and a smaller number leave it. He denies that they can count, but admits that ducks must have some sort of perception of numerosness, so that if the numbers involved are small enough, say two entering and one leaving, they may not be deceived, whereas a man having counted seventeen entering and sixteen leaving would realize that a dangerous hunter must still be inside.

But in Johnson's example it seems likely that the duck believes there is or is not a hunter still inside the blind, even though its ability to count may be very limited. There must be some upper bound to human abilities to make such counts; any of us might be confused if 4126 hunters entered the blind and only 4125 left, so that the distinction is a quantitative one. Thus such examples do not constitute valid evidence against the ability of animals to believe something simple and important in their lives. Johnson continues (p. 288) with the argument that "the crucial distinction between (human) belief and the superficially similar adaptive strategies of animals is that the former but not the latter involves use of explicitly entertained mental representations." The wording "explicitly entertained mental representations" seems to mean thinking consciously about one's beliefs, and Johnson claims that only human beings can do this. But how can anyone be so confident of this dogmatic negative assertion, especially when some animals communicate about what appear to be simple beliefs, such as the dancing bee that seems to believe there is a very desirable cavity at a certain distance in a particular direction?

Bennett (1964, 10) has also considered the question of animal communication from a philosophical viewpoint, with special emphasis on the dances of honeybees. He developed at length a philosophical argument "that honeybees are not rational creatures, and also that their dances do not constitute a language." Most of his argument was based on the fact that honeybee communication is not nearly as flexible and applicable to as wide a range of situations as human language. Bennett also doubted that bees could alter their communication rationally as a

result of unusual circumstances, such as the receipt of a message that the follower of a dance knew to be erroneous or implausible (Bennett 1964, 58). He did not consider the evidence that some bees react to dances on a swarm by changing their previously executed dance communication about a less desirable cavity to follow a more enthusiastic dancer and as a result visit and dance about the cavity she was describing. On returning from this cavity, the “convert” dances about it. This change of messages on the basis of information received from another’s dance seems rational, but Bennett was especially concerned with the possibility that bees might deny the message received by following waggle dances.

Gould (1984) and Gould and Towne (1987) have reported experiments in which something of the kind may actually have happened, although the data are not sufficient to provide a fully convincing case. Honeybees are reluctant to fly over water, and when hungry bees familiar with the local environment were exposed to waggle dances that signaled a food source in the middle of a small lake, many fewer left the hive than when they were stimulated by similar dances signaling food at equidistant locations over land. Other variables may have affected these results; but this type of experiment holds considerable promise for elucidating the degree to which honeybees may combine memories of topographical features with the information received from dances to guide rational responses to the messages they receive in this way. More recently Bennett (1988) titled his presidential address to the American Philosophical Association “Thoughtful Brutes,” in an obvious divergence from the views expressed by Malcolm fifteen years earlier. Recognizing the progress and promise of cognitive ethology, Bennett (1991) nevertheless emphasizes the serious philosophical difficulties that are encountered when we attempt to infer what nonhuman animals are thinking.

Premack, whose experiments with chimpanzees have demonstrated many of their mental abilities through carefully controlled experiments (Premack 1976), has argued that the dance communication of honeybees does not qualify as language, primarily because he considers it too rigid and inflexible. One of his comments is especially significant as an indication of the reluctance of inclusive behaviorists to appreciate the versatility of animal communication (Premack 1980, 212): “Ordinarily, the contrast between bee and human language is made on the grounds that only one of the two systems is learned, but this is a dubious contrast, since critical aspects of human language, including parts of both syntax and phonology, are probably not learned. More important, even if the bee’s unique system *were* learned it probably would not qualify as

language. The two systems can be better contrasted by asking if the bee shows any suggestion of representational capacity.”

Premack continues, “Suppose a scout bee were to gather information about the direction and distance of a food source from its hive. The bee encodes this information in its dance, and a second bee decodes the dance; but could the bee, when shown its own dance, judge whether or not this dance accurately represented the direction and distance of the source of food? Could the bee recognize that dance as a representation of its own knowledge? If a bee could judge between the real situation and a representation of that situation, it would be possible to interrogate the bee, just as we can interrogate the ape. A species that can be interrogated, such as the chimpanzee, is well on its way toward being able to make true-false judgments. But I know of no data that even faintly suggests that the bee can recognize the dance as a representation of its knowledge” (Premack 1980, 211–12).

When Premack speaks of showing a bee her dance, he implies presenting a visual representation. But bee dances ordinarily occur in the dark, and the information is transferred by tactile, acoustic, and chemical signals. Dancing bees often encounter other bees dancing about the same food source or cavity, and when a model bee such as that developed by Michelsen, Kirchner, and Lindauer (1989) has been perfected, a bee that has been dancing could easily be stimulated by dances of the model indicating either the same or different direction and desirability. Bees that are dancing about a particular location do not ordinarily become followers of “synonymous” dances conveying the same information, although Lindauer reported a few cases where a dancer changed role and became a follower of more enthusiastic dances of another bee reporting a better cavity. This differing behavior with respect to dances that are the same and those that are different from a bee’s own dances indicates recognition that the former are indeed representations of her own knowledge, while the latter are communicating a different message or thought. On balance, it is difficult to understand why Premack is so certain that honeybees lack any representational capacity, when their dances obviously do represent distance, direction, and desirability and convey such representations to others.

The explanation for this dogmatic negativity displayed by Premack and others such as Rosin (1978, 1980, 1984, 1988) or Wenner and Wells (1990) about the symbolic communication of honeybees probably lies in a deep seated reluctance to grant anything remotely comparable to human mentality to “lower” animals, as expressed in the following passage:

Mollusks, spiders, insects—invertebrates generally—differ from humans not in their lack of hard-wired components but in their lack of cognition. Griffin's phrase "cognitive ethology," when applied to invertebrates, appears to be a colorful misnomer rather like "tropical Norway" or the "nautical jungle." Vertebrates associate events not only on the basis of contiguity in space or time, but also on the basis of physical resemblance. Such species categorize or place "like" items together. . . . Invertebrates, presumably, could not be trained to demonstrate their comprehension of a rule instantiating physical similarity. (Premack 1986, 137–38)

Premack seems to be thinking of tasks in which objects are sorted, but equivalent judgments of physical similarity, or of belonging in a given category such as food or danger, must be very widespread in the natural lives of many active invertebrates.

The contemporary philosopher Daniel Dennett (1983, 1987, 1988) has advocated what he calls "the intentional stance" when analyzing not only human and animal cognition but also many examples of self-regulating inanimate mechanisms. As he defines it, "The intentional stance is the strategy of prediction and explanation that attributes beliefs, desires, and other 'intentional' states to systems—living and non-living." (Dennett 1988, 495). His insistence on including such simple devices as thermostats in this extended category of intentional systems leads him to deny any special status to conscious mental experiences. This denial of concern for subjective mental experiences is clearly articulated in responses to commentaries on his two articles in *Behavioral and Brain Sciences* (Dennett 1983, 380–84, and 1988, 538–39).

Dennett appears to be arguing that if a neurophysiological mechanism were shown to organize and guide a particular behavior pattern, this would rule out the possibility that any conscious mental experiences might accompany or influence such behavior. And he is closely enough akin to the positivists and behaviorists to base his inference of intentionality entirely on overt behavior. But, to quote Lloyd (1989, 191), "neurons take care of every need in every brain, so this argument for denying consciousness to the toad opens up to a slippery slope. Surely bats are open to the same counterargument, and . . . ultimately human beings." Dennett prefers a theoretical framework that encompasses the whole range of systems from thermostats to scientists or philosophers. Yet he applies terms that ordinarily refer to conscious mental states, such as belief and desire, even to thermostats. This amounts to a sort of semantic piracy in which the meaning of widely used terms is distorted by extension to paper over a fundamental problem—namely, the question whether conscious mental experiences occur in other species. Addi-

tional limitations of Dennett's position have been discussed by Baker (1987, 149–66).

Other contemporary philosophers have argued that the very notion of such conscious mental states as belief and desire is misguided and obsolete. Stich (1983) and Churchland (1986) have likened all consideration of such mental experiences to the phlogiston theory of combustion and to a belief in witchcraft. They and others apply the derogatory term “folk psychology” to any reliance on conscious mental experience in describing or explaining behavior. They confidently predict that a growing understanding of brain function will lead us to replace such mentalistic terms with specific neurophysiological concepts that refer to the brain functions leading to particular sorts of behavior.

A serious weakness with such arguments is that none of the required neurophysiological mechanisms has yet been identified. We are asked to replace valid and useful terms and concepts with what have been called “promissory notes,” that is, unspecified physiological mechanisms that it is said will be discovered in the uncertain future. This difficulty has left many philosophers and neuroscientists unpersuaded by the arguments of Churchland and Stich, for example, Routley (1981), Double (1985), Horgan and Woodward (1985), Jeffrey (1985), Russow (1986), Sanford (1986), Baker (1987), Clark (1987, 1989), Stent (1987), Putnam (1988), and Radner and Radner (1989). Of course, brains or central nervous systems in general are the organs of thought. But to discard useful concepts about mental states because it is anticipated that the neurophysiological mechanisms underlying them will someday be discovered is a misleading device to escape from challenging problems by shifting them to an inaccessible future. Furthermore, the elucidation of the mechanisms by which an important process is carried out does not eliminate the process itself or render it unimportant. For example, the magnificent discoveries of molecular genetics have not eliminated heredity or rendered the term useless or misleading in any way. Likewise, if and when a neural basis for belief or desire is discovered, this will be a comparably significant advance, but will not render obsolete these important attributes of conscious thinking.

### Self-awareness and Ethical Issues

Hardly anyone denies that there is a large ethical difference between torturing a dog or monkey and mutilating even the most elaborate and efficient machine. The latter act may be wasteful or pernicious because it damages something useful or beautiful; but it is not wrong in the



same sense as inflicting needless pain. But we can scarcely escape all responsibility for activities that directly or indirectly cause the injury, death, and suffering of other animals. For instance, even the most confirmed vegetarian would find it difficult to avoid eating vegetables that have been protected by insecticides or other agricultural practices that cause the death of insects that would otherwise have eaten the plants in question.

Thus we are all obliged to make value judgments about what activities are permissible even though they are harmful to animals, and such decisions are often based on the degree to which we believe that various animals suffer consciously. These are difficult decisions, primarily because we know so little about the feelings and thoughts of other species, but choices must be made about the severity or the importance of animal suffering. For example, we generally exert greater care to avoid hurting mammals and birds than fishes or invertebrates, and most rules about animal welfare apply primarily or exclusively to warm-blooded animals, as discussed by Burghardt and Herzog (1980). But how do we know whether some species suffer more than others? We have so very little firm knowledge on which to base decisions and trade-offs concerning animal welfare that whatever can be learned about the subjective feelings and thoughts of animals has a direct relevance to these sorts of value judgments.

Many of the philosophers who have considered this matter feel obliged to define mental capabilities that are unique to our species, and to rely on these as moral justification for treating people very differently from animals. One of the more extreme examples of this position was the argument advanced by Adler (1967) that if it should be found that animals differ from men only in degree and not radically in kind, such knowledge would destroy our moral basis for holding that all men have equal basic rights (267–68). Like many others, he considered human language as the primary distinguishing attribute that sets us apart from all other animals. Admission that any animal could communicate intentionally therefore appeared to undermine our moral and ethical standards.

Earlier in the same book Adler dismissed the dance communication of honeybees as “a purely instinctive performance on their part (that) does not represent, *even in the slightest degree*, the same kind of variable, acquired or learned, and deliberately or intentionally exercised linguistic performance that is to be found in human speech” (italics in original, 114–15). He was concerned primarily with early claims that dolphins communicated by means of something approaching human language;

but the more recent discoveries about the versatility of communication in both dolphins and the Great Apes pose the same basic question even more emphatically. For there can remain no doubt that these sorts of communicative behavior are variable and acquired or learned, so that the general position advocated by Adler and others would now have to rely on the claim that nonhuman animals do not communicate deliberately or intentionally. This claim in turn requires that we deny any conscious intent to all communicating animals, a dubious assertion to say the least.

Allen (1987, 158–59) has extended Adler's type of argument by adding a political twist: "To blur the distinction between animal and human, especially by distorting the biological reality (or by claiming for the biological reality more than it can offer), is to play into the hands of a political mood that leads ultimately to fascism; . . . [it] paves the way for relegating some people to the subhuman category on the basis of their biology. Once there, the usual moral restraints and considerations cease to apply, and fascism has arrived." In other words cognitive ethology should not be investigated, lest the results undermine our moral standards, a view that is reminiscent of the outrage that greeted Darwin's recognition of biological evolution. Fortunately these imagined threats to morality proved exaggerated in the nineteenth century, and there is no reason to expect a different outcome now. Morals and ethics should surely be based on accurate understanding of the relevant facts, and since they have survived the Copernican and Darwinian revolutions, strengthened rather than weakened by correction of factual errors, there is no reason to fear a different outcome once evolutionary continuity of mentality is recognized.

More recently Carruthers (1989) has argued that only if creatures are capable of thinking consciously about their own thoughts, and of reporting what they think, do they deserve sympathy and moral concern. If their thoughts and suffering are not accessible to reportable reflective consciousness (Natsoulas's *Consciousness* 4), Carruthers argues (268–69),

since their experiences, including their pains, are nonconscious ones, their pains are of no immediate moral concern. Indeed, since all the mental states of brutes are nonconscious, their injuries are lacking even in indirect moral concern. . . . Much time and money is presently spent on alleviating the pains of brutes which ought properly to be directed toward human beings, and many are now campaigning to reduce the efficiency of modern farming methods because of the pain caused to the animals involved. If the arguments presented here have been sound, such activities are not only morally unsupportable but morally ob-

jectionable. . . . Since their pains are nonconscious ones (as are all their mental states), they ought not be allowed to get in the way of any morally serious objective.

Even though Carruthers considers human infants to be non-conscious, that is, to lack reflective consciousness, they are granted moral status because they will later be capable of such consciousness. Presumably he would be obliged to conclude that a newborn baby suffering from an incurable defect that is absolutely certain to kill him before he can achieve reflective consciousness would therefore revert to the nonconscious status to which Carruthers assigns almost all animals, and thus become available for the same justifiable abuses. This is reminiscent of the Port Royal followers of Descartes who are said to have tortured animals with the confident conviction that their cries of agony were comparable to the noises from machinery.

Opposed to the views of Adler, Johnson, and Carruthers are the thoughtful analyses of philosophers such as Routley (1981), Midgley (1978, 1983), Jeffrey (1985), Rollin (1989, 1990), Radner and Radner (1989), and Dupré (1990), all of whom seriously explore both the indications that many animals are conscious, and the philosophical and sociological factors that may help explain the widespread reluctance to give adequate weight to this evidence. These philosophers and many scientists see no reason to place such overwhelming emphasis on the distinction between perceptual and reflective consciousness. The latter is in one sense a simple form of introspection, and, as discussed in chapter 1, it is somewhat ironic that after the longstanding rejection of introspection as a source of reliable evidence about the workings of our minds, this special form of introspection should be elevated to such a crucial status as a litmus test for humanity and moral status.

This distinction between perceptive and reflective consciousness is somewhat akin to the question of self-awareness. If we grant that some animals are capable of perceptual consciousness, we need next to consider what range of objects and events they can consciously perceive. Unless this range is extremely narrow, the animal's own body and its own actions must fall within the scope of its perceptual consciousness. As pointed out in chapter 1, there is no part of the universe that is closer and more important to an animal than its own body. But those who hold that self-awareness is a unique human attribute often fall back to an insistence that although animals may be perceptually conscious of their own bodies, they nevertheless cannot think such thoughts as "It is I who am running, or climbing this tree, or chasing that moth."

Yet when an animal consciously perceives the running, climbing, or moth chasing of another animal, it must also be aware of who is doing these things. And if the animal is perceptually conscious of its own body, it is difficult to rule out similar recognition that it, itself, is doing the running, climbing, or chasing. If we grant that animals are capable of perceptual awareness, denying them some level of self-awareness would seem to be an arbitrary and unjustified restriction. An example of the difficulties that arise when one denies any sort of self-awareness to animals has been pointed out to me by Lance A. Olsen, who has been impressed by the tactics of grizzly bears in seeking out positions from which they can watch hunters or other human intruders without allowing themselves to be seen, as has been described by Haynes and Haynes (1966), Mills (1919), and Wright (1909). It has also been reported that these bears make efforts to avoid leaving tracks, indicating that they realize that their tracks may be followed by hunters. Concealment by moving behind something opaque would require only simple behavior patterns. A simplistic interpretation might be that the animal moves behind as much vegetation as possible while still being able to see out. But they sometimes seem to do this without exposing any part of their body to view, suggesting some such thought as "I must get *my* whole body behind these bushes."

The question of self-awareness is one of the very few areas of cognitive ethology where we have some concrete experimental evidence. Gallup (1977, 1983) and Suarez and Gallup (1981) have demonstrated that some chimpanzees can learn to recognize mirror images as representations of their own bodies. After becoming familiar with mirrors, chimpanzees were anesthetized, and while they were unconscious a mark was placed on a part of the head that they could not see directly. On awakening they paid no attention to the mark until a mirror was provided, but then they touched it and gave every sign of recognizing that it was on their own bodies. Although orangutans also used mirrors in this way, extensive efforts to elicit such responses from monkeys, gibbons, and even gorillas have failed. These and all other animals generally react to their mirror image as though it were perceived as another animal, if they pay any attention to it at all. For example, in recent experiments reported by Povinelli (1989), elephants learned to use mirrors to locate hidden food, but showed no signs of self-recognition, according to Gallup's criterion. Gallup (1983) argues that self-awareness is the criterion of mind, but believes that dolphins and elephants can also monitor their own mental states. He appears to be somewhat troubled to find himself appealing to a form of introspection as a crucial crite-

tion, in view of the fact that experimental psychologists long ago abandoned introspection as a source of data about the workings of the human mind.

It is difficult to be certain whether the failure of most animals to recognize mirror images as representations of their own bodies demonstrates that they are incapable of self-awareness, as Gallup claims, or whether they fail for some other reason to correlate the appearance and movements of the mirror image with those of their own bodies. Especially puzzling is the failure of gorillas to learn mirror self-recognition, since in most other ways they seem just as versatile and intelligent as chimpanzees and orangutans. Nevertheless only our species, chimpanzees and orangutans have been clearly demonstrated to be capable of recognizing that a mirror image depicts their own bodies.

Both reflective consciousness and self-awareness are often held to be uniquely human attributes. It remains an open question whether we can ascertain which animals experience even perceptual consciousness, although the weight of evidence reviewed in previous chapters suggests that they often do. But what sorts of evidence might indicate whether or not they think about their own thoughts? One suggestive indication is provided by memories and expectations. When an animal performs complex and demanding learned behavior it may be thinking consciously about events that it remembers and that have resulted in its learning, for example, what to do in order to obtain food or avoid some unpleasant stimulus. If so, the animal may be reacting to the mental image or representation of itself in the situation in which it learned what to do, or what to expect.

Behaviorists will of course object that learned behavior need not be accompanied by conscious memory. But a heron fishing with bait, or a pigeon succeeding in the concept recognition experiments described in chapter 6 may well be consciously aware of a relevant memory rather than blindly acting out a complex pattern of learned behavior. And when an animal communicates about something it consciously remembers or anticipates, this communication can appropriately be viewed as a report about some of its thoughts. Many psychologists have followed the lead of Tolman (1932, 1937) in studying expectancies, although the customary behavioristic inhibitions have almost always led them to avoid any hint of conscious anticipation on the animal's part. But it may be that we have seriously overlooked abundant, if less than totally definitive, evidence that animals do think about their simple thoughts, and communicate some of these thoughts about thoughts to others.

I will not attempt to advocate how best to resolve the conflicting

motivations that necessarily confront us with respect to the treatment of animals. These are fundamental moral judgments, which can be helpfully informed by scientific understanding, but fall outside the proper scope of purely scientific analysis. No one seriously advocates harming animals just for the sake of doing so, although thoughtless cruelty is unfortunately prevalent in some circles. What scientific understanding can provide is evidence against the notion that all animals are incapable of suffering and therefore totally undeserving of sympathy. That idea seems unsupportable on any scientific grounds, and abhorrent as well. Ethics and morals should be based on positive values, rather than merely on the exclusion of supposed inferiors. The important and difficult questions do not concern extreme examples but borderline cases and practical trade-offs, as thoughtfully discussed by Bekoff and Jamieson (1991). How much animal suffering is justified in order to grow crops, eat meat, enjoy hunting or fishing, conduct physiological or behavioral research, test new cosmetics, develop new surgical techniques before they are tried on human patients, or use animals in innumerable other ways that benefit people to varying degrees? I do not feel that scientists have any special right to advocate moral judgments in such difficult matters, but cognitive ethology does hold out the prospect of providing helpful information and understanding that can lead to better informed decisions.

Some activities have relatively minor adverse effects on animals and pay large dividends in human benefits. To test promising new surgical procedures on deeply anesthetized rats that otherwise have lived reasonably optimal lives seems a justifiable trade-off. But crippling an elephant and leaving it in agony while the nineteenth-century hunter enjoyed his tea, as described by Midgley (1983, 14–17), was clearly an unwarranted indulgence in minor human satisfaction at the expense of considerable suffering. Most cases fall somewhere between such extremes, and can be decided only by weighing the magnitudes of both the human benefit and the animal suffering. This leads to the further and difficult question of the degree to which particular animals suffer when treated in various ways. It is customary to assume that mammals and birds are more deserving of sympathetic treatment than fishes or insects. And even the most extreme advocate of animal rights is unlikely to mourn the apparent extinction of the smallpox virus.

But how can we estimate the degree to which various kinds of animals suffer when injured in particular ways? Only as we learn more about their subjective mental experiences will it be possible to do this on an informed basis. This is a tremendous challenge, and we are at

present so extremely ignorant about the conscious mental experiences of animals that it will be a long time before scientific methods can be developed to measure just how much a given animal suffers under particular conditions. But a beginning has been made by the types of experiment reviewed by Dawkins (1980, 1990) in which animals are allowed to choose between various environmental situations, such as sizes and types of cages. There are many uncertainties in such investigations, but they certainly point in the right direction. Because we know so little, significant surprises may await future investigators. For example, it might turn out that some treatments that seem at first glance to be detrimental are actually preferred by the animals; and insofar as this may be the case, such information could be appropriately used in weighing the conflicting demands of human benefit against animal deprivation or suffering. But this is almost idle speculation in our current state of ignorance, and I can best conclude this section by reiterating that whatever we can learn about the subjective mental experiences of animals has significant potential relevance to ethics of animal utilization by our species.

### Scientific Significance

The whole kingdom of nonhuman animals, comprising millions of species and literally countless numbers of individuals, is clearly an important component of our planet, for the universe would be a very different one if they did not exist. For that reason alone it is important to understand animals as fully as possible; for without such understanding we will remain blind to an important aspect of reality. We cannot understand animals fully without knowing what their subjective lives are like. Until this is possible, and at present it is possible only to a very limited degree, we will remain unable to appreciate adequately either the nature of nonhuman animals, or how we differ from them. This zoological significance of the question of animal consciousness may lack the practical urgency of the ethical questions, and it may not appeal to philosophers as an intellectual challenge comparable in significance to the general problem of other minds. But it not only bears directly on the philosophical and ethical issues outlined above; it is also, in its own right, an important reason to inquire as deeply and critically as we can into the subjects discussed in this book.

Much of twentieth-century science has gradually slipped into an attitude that belittles nonhuman animals. Subtle but effective nonverbal signals to this effect emanate from much of the scientific literature.

Physical and chemical science is assumed to be more fundamental, more rigorous, and more significant than zoology. Modern biology revels in being largely molecular, and this inevitably diverts attention away from the investigation of animals for their own sakes. Part of this trend may be due to an unrecognized reaction against the deflation of human vanity by the Darwinian revolution. The acceptance of biological evolution and the genetic relationship of our species to others was a shattering blow to the human ego, from which we may not have fully recovered, for it is not easy to give up a deep seated faith that our kind is unique and qualitatively superior. A psychological palliative that may be subconsciously attractive, even to many scientists, is to shift attention away from the embarrassing fact of our animal ancestry by accentuating those aspects of science that are more akin to physics. This may help explain why so many appear to be so certain that consciousness and language are uniquely human capabilities and that the discovery of symbolic communication by honeybees "upsets the very foundation of behavior, and biology in general" (Rosin 1978, 589). Quite the contrary, such discoveries in the field of cognitive ethology extend and improve our understanding of animals; a definition of biology that rules out those discoveries *a priori* suffers from self-inflicted impoverishment.

The principal counterweight to the myopic intolerance so prevalent in contemporary molecular biology is provided by evolutionary biology which seeks to explain as many attributes of living organisms as possible in terms of their contribution to survival and reproduction, that is, to their evolutionary fitness. This presents many difficult challenges, because so many interacting variables affect the lifetime success and reproduction of most animals. A basic assumption underlying most of evolutionary biology is that various sorts of animals survived and reproduced better than others *in the past*. But there are hardly ever any directly relevant data available to show just how the ancestors of contemporary animals actually outperformed others. For example, it seems clear that placental mammals are generally more efficient than the marsupials. But if a skeptic asks just how we know this, zoologists must fall back on indirect evidence to support the inference, such as the disappearance of many marsupials from the South American fauna at about the time that a new land bridge at Panama allowed placental mammals to reach that continent. Of course, no zoologist was present to observe just what the placentals did better than the marsupials. But convincing conclusions can be reached even in the absence of ideally pertinent data.

Evolutionary biology has been so concerned with identifying how the structure, function, and behavior of animals contribute to their fit-



ness that it has tended to underemphasize those attributes that render animals importantly different from nonliving systems, plants, or protozoa. Independent mobility and a heterotrophic metabolism dependent on food materials synthesized by plants are the most obvious distinguishing features of multicellular animals. But animals are also clearly more than mobile metabolisms. They appear to *act*, that is, to do things spontaneously, on their own. What they do is determined in large part by outside influences; yet the complexity and the remoteness of animal actions from whatever external causes may be at work distinguishes them in an important fashion from microorganisms, plants, or physical systems. Most of these spontaneous activities are regulated by central nervous systems, and such systems, together with the adaptable behavior they make possible, are a special feature of living animals not found elsewhere in the known universe. In addition, members of at least one species also experience subjective feelings and conscious thoughts. We cannot be certain how common this additional feature actually is; but suggestive evidence such as that reviewed in this book makes it at least plausible that simple forms of conscious thinking may be quite widespread.

### Conscious Instincts

There is a strong tendency among contemporary behavioral scientists to assume that conscious mental states, on the one hand, and learning or evolutionary selection, on the other, are mutually exclusive alternatives. But this is by no means self-evident. An animal may or may not be conscious, and its behavior may be influenced to varying degrees by genetic programming. These are actually quite independent considerations, and any combination is possible. Learned behavior is not always consciously acquired or executed, even in our own species, and it may be even less closely linked to conscious awareness in nonhuman animals. Likewise, a genetically programmed behavior pattern may or may not be accompanied or guided by conscious thinking. There is no reason why genetic influences should not lead to a central nervous system that develops conscious thoughts, especially when such thinking is adaptive and has been selected in the course of the animal's evolutionary history. In short, the customary assumption that if some behavior has been genetically programmed, it cannot be guided by conscious thinking, is not supported by any solid evidence.

To many inclusive behaviorists, the belief that a behavior pattern has

been selected in the course of evolution seems to rule out any possibility that it can be accompanied or influenced by conscious thinking. Skinner (1988, 78) has stated this view in characteristically concise and explicit terms: "Complex repertoires of behavior are shaped and maintained in strength with appropriate contingencies of reinforcement. Behavior once attributed to feelings and states of mind can then be explained in a simpler way. Once that is done, it is easier to suppose that complex genetic repertoires also do not require feelings and states of mind. . . . We have no more reason to say that an individual designs its own behavior than to say that a species does, and no more reason to say that a species designs its behavior than that it designs the nerves and muscles with which the behavior is executed." This assertion of absolute determinism implies that our conscious thinking cannot affect our behavior any more than we can wish ourselves wings in place of arms. Yet this compulsive parsimony has long since been rejected as grossly inadequate to account for human behavior and mentality, especially our use of language. As we learn more about the versatility of animal behavior, I believe that we will outgrow behaviorism for the same general reasons.

Once we accept the basic materialistic assumptions expressed in chapter 1, it follows that conscious thoughts and subjective feelings are caused by events in central nervous systems. Although we cannot rigorously prove that all the critically causal events take place in the central nervous system, everything we know about neurophysiology points in that direction, even though a normally functioning brain must operate in close harmony with the rest of the body. Kidneys, arteries, and adrenal glands are also necessary for consciousness, but in a supporting role. We know next to nothing about how brain functions that do lead to human consciousness differ from those that do not. We can of course make general inferences that certain parts of the human brain, such as the cerebral cortex or reticular system, are more important than others for conscious thought, but all known structures and functions of neurons and synapses seem to be much the same wherever they occur, whether in different parts of the human brain or in other brains. It seems highly unlikely that there are "consciousness neurons" or specific biochemical substances such as neurotransmitters, that are uniquely correlated with the conscious state, and that a person is conscious when and only when these cells are activated or these substances are present. It seems far more likely that consciousness results from patterns of activity involving thousands or millions of neurons.

Most of our physiological functions proceed smoothly without our

conscious awareness. These functions have reached this efficient state through the growth and integration of millions of cells following the genetic instructions transmitted from one generation to the next by DNA. Having recognized this, and having learned that much of animal behavior is under genetic control, we have concluded that it must lack any accompanying consciousness. For instance, many insects and spiders carry out quite elaborately integrated patterns of behavior, and they do so almost perfectly on the first appropriate occasion, without any opportunity to learn what to do. This absence of learning is then taken, almost universally, as proof that the animal has no conscious awareness of its instinctive behavior. This subject is rendered somewhat complicated by the great difficulty of teasing out the relative importance of genetic and experiential components influencing a given pattern of behavior. Species specificity, near constancy of a given behavior among all members of a species, does not necessarily mean that no learning is involved, because members of the species may be exposed to very similar environmental influences during development. In a few cases where the evidence is reasonably complete and satisfactory, it seems that the genetic instructions are rather general and that the individual animal learns the specific and essential details.

Perhaps we should pull back for a moment and ask ourselves just what evidence supports this deep-rooted assumption that only learned behavior can be accompanied by conscious thinking. This belief arises, I suspect, from analogies to our own situation. Human lives clearly require an enormous amount of learning, so much so that many have denied the existence of instinctive, genetically programmed human behavior. It is widely believed that only the simplest human reactions such as eye blinks, knee jerks, sneezing, cries of pain, exclamations one makes when startled, or a newborn baby's suckling are under predominantly genetic control. Many of these reactions happen automatically, unintentionally, and without any learning, although we may be aware of them as they occur. We do not plan to sneeze although we certainly know we are sneezing. But we may not even realize that we have blinked in response to a flash of light or the sight of something moving rapidly toward us. From these experiences we reason that when animal behavior requires no learning it cannot be accompanied by conscious thought.

Consciousness of one's bodily activities falls into two general categories: we may consciously anticipate, plan, and intend to perform some action, or our bodies may simply do something without any con-

scious expectation and perhaps without our being able to affect the action. Yet even in the second case we may be completely conscious of what our body is doing. A typical case of the first type is reaching out to grasp something; this usually entails consciously deciding to pick up the object, although it may also occur unconsciously or even involuntarily. The second category might be exemplified by the withdrawal response to a painful stimulus. Such simple human reflexes have tended to serve as "type specimens" of instinctive behavior and to color our view of unlearned behavior as a whole. But perhaps it is unwisely anthropocentric to assume that this view accurately describes instinctive behavior in all other animals. The large genetic component underlying many sorts of animal behavior may not justify the conclusion that all instinctive behavior is a homogeneous category. In particular, the analogy to our own situation does not establish how tightly consciousness is linked to learned behavior as contrasted with behavior strongly influenced by hereditary constitution.

When animals behave instinctively, they might be fully aware of what they are doing, without necessarily having experienced a prior intention, still less understanding the causes of their behavior or its ultimate consequences. Our own conscious thoughts need not be tightly linked to any overt behavior at all. We can think about objects and events, including past or future activities, without doing anything. It can be argued that our previous learning has led indirectly to such unexpressed thoughts, yet we certainly experience conscious thoughts that are unrelated to any current behavior or sensory input. Recognizing this obvious fact, it is appropriate to inquire whether conscious thoughts might sometimes arise as a result of the brain's genetically guided development and functioning.

Might a brain attain the state necessary to produce conscious thoughts without prior stimulation by any sensory input comparable to the content of the thought?

These considerations lead to the fundamental question whether only learned behavior can be accompanied by conscious mental experiences. I have reviewed many cases of animal behavior that appears so versatile and so appropriately adapted to unpredictable circumstances that it seems likely to be accompanied and guided by simple conscious thinking. Such versatility is very often based on the application of learned knowledge, but this may be neither a sufficient nor a necessary condition in any absolute sense. Animals may "figure out" what will get them things they want even when the knowledge needed for such thinking

about probable future events has not been learned in any direct and explicit sense. A good example is the apparent insight displayed by Heinrich's string-pulling ravens discussed in chapter 5.

## Animal Dreams and Fantasies

The subject of animal thinking is usually discussed by Western intellectuals who try hard to be objective and realistic. But the content of much human consciousness does not conform to objective reality. Fear of ghosts and monsters is very basic and widespread in our species. Demons, spirits, miracles, and voices of departed ancestors are real and important to many people, as are religious beliefs that entail faith in the overriding significance of entities that lie far outside of the physical universe studied by objective science. Yet when we speculate about animal thoughts, we tend to assume that they must necessarily be confined to practical down-to-earth matters, such as how to get food or escape predators. We usually suppose that animal thinking must be a simpler version of our own thinking about the animal's situation.

But there is really no reason to assume that animal thoughts are rigorously realistic. Apes and porpoises often seem playful, mischievous, and fickle, and anything but businesslike, practical, and objective. Insofar as animals think and feel, they may fear imaginary predators, imagine unrealistically delicious foods, or think about objects and events that do not actually exist in the real world around them. The young vervet monkey that gives the eagle alarm call for a harmless songbird may really fear that this flying creature will attack. As we try to imagine the content of animal thoughts, we should consider the possibility that their thoughts, like some of ours, may be less than perfect replicas of reality. Animals may experience fantasies as well as realistic representations of their environments.

The recognition that animal thinking may not always be strictly realistic leads to the subject of animal dreams. Darwin and many others have been impressed by the fact that sleeping dogs sometimes move and vocalize in ways that suggest that they are dreaming; their movements resemble those of feeding, running, biting, and even copulation. They sometimes snarl and bark. Some observers of sleeping animals have concluded that these motions and vocalizations accompany dreams related to recent experiences. Human sleepers show two types of sleep when analyzed by an electroencephalogram. The first, a relatively low-frequency pattern, characterizes deep sleep; the second, called REM sleep, is more irregular and is usually accompanied by rapid eye move-

ments (REMs), which can be recorded separately by electrodes near the eyes. When human subjects are awakened from these two types of sleep, they are more likely to report that they were dreaming during REM sleep (Fishbein 1981; Morrison 1983). Comparable recordings from sleeping birds and mammals show similar patterns of REM sleep (Hartman 1970; Jouvet 1979; Cohen 1979), indicating that they also dream. A number of recent theories about the function of dreaming have been reviewed by Winson (1985) without resolving the question definitively. But whatever its functional utility, dreaming seems to be widespread, at least among mammals.

A few rather limited studies of human eye movements during REM sleep suggest that the movements resemble those that would be expected during the activity or experience about which the person is dreaming. For instance, dreaming about a tennis match might produce repeated eye movements back and forth from side to side as the dreamer follows the tennis ball. But such experiments have not been developed into a reliable procedure for monitoring the content of human dreams, so dreaming dogs or other animals cannot yet be studied in this way. But if it could be perfected, such monitoring might allow us to determine what the animal is dreaming about. We might then be able to study a type of mental experience that exhibits an extreme form of displacement. For nothing in the sleeper's immediate environment ordinarily corresponds to the content of the dream. Stoyva and Kamiya (1968) proposed that a combined analysis of electrical recording of eye movements and subsequent verbal reports of dream content might eventually lead to objective investigations of human mental experience. But behaviorists have been characteristically uninterested in pursuing this approach. Although we can easily imagine experiments along the lines outlined above that might yield verifiable objective evidence, too few have been carried out to permit any firm conclusions. Perhaps a combination of cognitive ethology and cognitive neurophysiology will eventually fill this gap and provide empirical evidence about the reality and content of animal dreams. It would indeed be ironic if evidence that animals think consciously should come to be derived from an understanding of their dreams.

The emergent property of consciousness confers an enormous advantage by allowing animals to select those actions that are most likely to get them what they want or to ward off what they fear, as suggested in chapter 1. To paraphrase Karl Popper, animals that think consciously can try out possible actions in their heads without the risk of actually

performing them solely on a trial-and-error basis. Considering and then rejecting a possible action because one decides it is less promising than some alternative is far less risky than trying it out in the real world, where a mistake can easily be fatal. We carry out such trial-and-error behavior in our minds, and it is difficult to avoid the conclusion that animals often do something similar at a simple level. This activity, attribute, or capability is a truly marvelous phenomenon. Although almost all discoveries about animal behavior throw some light on animal mentality, scientists have devoted relatively little attention to it, at least in direct and explicit form. Once its significance is appreciated more fully, there is good reason to hope that we can learn much more about it.

I am confident that with patience and critical investigation we can begin to discern what life is like, subjectively, to particular animals under specific conditions, beginning with the sorts of evidence reviewed in previous chapters. Cognitive ethologists can certainly improve greatly on these preliminary inferences, once the creative ingenuity of scientists is directed constructively toward the important goal of answering Nagel's basic question: What is it like to be a bat, or any other animal? Contrary to the widespread pessimistic opinion that the content of animal thinking is hopelessly inaccessible to scientific inquiry, the communicative signals used by many animals provide empirical data on the basis of which much can reasonably be inferred about their subjective mental experiences. Because mentality is one of the most important capabilities that distinguishes living animals from the rest of the known universe, seeking to understand animal minds is even more exciting and significant than elaborating our picture of inclusive fitness or discovering new molecular mechanisms. Cognitive ethology presents us with one of the supreme scientific challenges of our times, and it calls for our best efforts of critical and imaginative investigation.

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