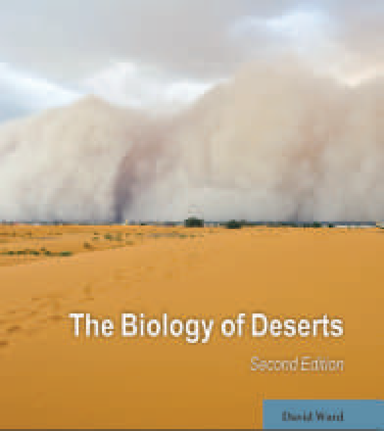

The Biology of Deserts

Second Edition

David Ward

Biology of Habitats

The Biology of Deserts

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To my wife, Megan, who contributed to this book in so many ways

Preface to the First Edition

Deserts are difficult to define. They vary greatly in their aridity, from close to 0 mm of rainfall annually to more than 500 mm. They range in temperature from more than 50°C to far less than 0°C. Most of all, they are distributed across the globe in so many places that it is difficult to define exactly where they are and what makes a desert what it is. I have used the term 'desert' in the broadest sense of the word, but have tried to keep away from neighbouring topics such as savannas and grasslands. I have usually used the term to include all 'arid' and 'semi-arid' habitats, or where the term 'xeric' seemed to fit. Most of all, I have tried to focus on the studies that use the term prominently, especially where I am familiar with the system.

The amount of research done varies greatly among deserts, and often there is a difference in the issues that are focused on in a particular region. North Americans have done more work of interest in terms of evolutionary studies and population and community ecology. Israeli scientists have done a lot of research on population and community ecology, as well as ecosystem and conservation ecology. Researchers in Russia (and allied states) and China have mostly been concerned with applied issues, as have researchers in many Arab states and Iran and India. Researchers in Australia have focused a lot on rangelands as well as on plant, lizard, and small mammal diversity. Southern Africans have focused on a range of issues, especially on animal physiology and plant diversity, but very little has been done on plant physiology and population and community ecology. In contrast, German researchers have extensively studied desert plant physiology in the Sahara, Middle East, and the Namib and Kalahari deserts. South Americans have conducted studies on a wide range of desert issues, with a focus on population ecology. Clearly, if we each learned a bit from each other, we could gain a lot more insight into how desert systems work. It is not possible to assume that if a trend has been demonstrated elsewhere, it will work the same way in all deserts. I believe that we need to consider how we might replicate studies in different deserts (e.g. plant and animal physiology studies) and expand the number of deserts in which we study competition, facilitation, predation, parasitism, and plant–animal interactions (as well as ecosystem studies).

In this book, I have decided to focus on an evolutionary approach to deserts because I believe that this is what makes them so interesting. Deserts are indeed laboratories of nature. I realize that evolution means different things to different people. Here, I use the term very broadly, covering phylogenetic constraints, optimization, and convergence, among other things. This is not to say that there is no coverage of other issues. I believe that I would be doing a disservice if I were to focus on evolutionary issues alone, so I do cover ecosystem approaches, desertification, and conservation issues, to name but a few. However, there are other excellent books published on community and ecosystem approaches such as Gary Polis' (1991) *Ecology of Desert Communities*, Walt Whitford's (2002) book on *Ecology of Desert Systems*, and many others covering specific deserts. I particularly like John Sowell's (2001) book titled *Desert Ecology: An Introduction to Life in the Arid Southwest*. Clearly, its focus is on North American deserts, but it covers a tremendous range of issues. These are all very good books; it will be hard to find a niche among them.

There are many people that I would like to thank. Most of all, I thank my wife, Megan Griffiths-Ward, for her help in copy-editing (and Maureen Ward and Betsy Griffiths) and in so many other ways. Elizabeth and Jonathan Griffiths were very kind to us in Gettysburg. I thank my colleagues at the Blaustein Institutes for Desert Research in Sede Boqer, Israel, including my long-time collaborator and friend, David Saltz, as well as Zvika Abramsky, Yoav Avni, Yoram Ayal, Burt Kotler, Boris Krasnov, Yael Lubin, Ofer Ovadia, Berry Pinshow, Uriel Safriel, Moshe Shachak, Jura Shenbrot, Josef Plakht, Eli Zaady, and Yaron Ziv. I pay special thanks to my technician of many years, Iris Musli. I am indebted to my many Israeli students, especially Gil Bohrer, Keren Or, Natalia Ruiz, Madan Shrestha, and Sergei Volis. In South Africa, I am very grateful to my research assistant, Vanessa Stuart, my German collaborator, Kerstin Wiegand, and my students, especially to Tineke Kraaij, Mari-Louise Britz, Khanyi Mbatha, and Michiel Smet, as well as to Katrin Meyer, Aristides Moustakas, and Jana Schleicher. Last, but definitely not the least, I would like to thank my editor, Ian Sherman, and his assistant, Helen Eaton, at Oxford University Press for their inspiration and assistance.

Preface to the Second Edition

A major difference in this second edition is that I have tried to emphasize the role of global changes and desertification more than in the first edition. In my opinion, too much emphasis has been placed on global warming and not global changes per se. While, ultimately, the world will continue to heat up as fossil fuels are burned, many people struggle to understand that it is human-induced changes in the world rather than a simple case of warming that is likely to occur. Thus, decreases in temperature and increased rainfall are also consequences of the ways that we are altering our world. Among these varied effects, desertification is often among the most egregious. Desertification usually occurs on the periphery of deserts, leading ultimately (and unfortunately) to the increasing size of arid and semi-arid regions. Hopefully, more researchers and policy-makers will take up the defence of deserts and means of combatting desertification. The cause is usually due to one effect or another of an increase in human population sizes. Controlling human population sizes is likely to be a very slow process, if it happens much at all. Hence, we need to strive to minimize the effects of desertification on our environments by increasing our efficiency of resource use. I have also tried to link the chapters on plant and animal physiology more than in the first edition through emphasis on heat shock proteins. In this second edition, I have updated many of the references I believed important to change. Science is, of course, a continually progressive topic that is always in need of updating. However, there are also many things that have stood the test of time—these references I have retained.

In South Africa, I am very grateful to my research assistant Kayleigh Muller, my long-time German collaborator, Kerstin Wiegand, and my students, especially to Tiffany Pillay, Admore Mureva, Desale Okubamichael, and Snehalatha Vadigi. I thank Stephan Getzin of Göttingen University for providing me with photographs and advice. I thank my colleagues at the Blaustein Institutes for Desert Research in Sede Boqer, Israel, including my long-time collaborator and friend, David Saltz, as well as Burt Kotler, Boris Krasnov, Yael Lubin, Ofer Ovadia, and Berry Pinshow. I am also grateful to Tony Verboom, Michael Cramer, and Timm Hoffman at the University of Cape Town, Ian Wright from Macquarie University, and Willie Stock from Edith Cowan University in Australia and Doug Kelt from the University of California at Davis for their advice and assistance. I thank too the various people who provided photographs and figures, including Gidske Andersen, Trine Bilde, Wolfang Bodenmüller, Eli Greenbaum, Aaron Greenville, Yael Lubin, Doron Nissim, Julián Padró, Michal Samuni-Blank, Adrian Shrader, Alon Ziv, and Leo Zwarts. I am most grateful to the

School of Life Sciences (especially Richard Beckett) at the University of KwaZulu-Natal for granting me sabbatical leave. I am thankful to the Biology Department at Gettysburg College during my sabbatical there, to my host Veronique Delesalle, for her assistance and collegiality, and to Janelle Wertzberger and the staff of ILL of the Gettysburg College Library for their tremendous assistance with tracking down articles. I am also grateful to my colleagues at Kent State University, especially Laura Leff, for giving me time to complete this edition. I thank Charles Lauder and Indu Srinivasan for their attention to detail prior to publication. Last, but definitely not the least, I would like to thank my editor, Ian Sherman, and his assistant, Lucy Nash, at Oxford University Press for their inspiration and assistance.

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1 Introduction

> Nothing in biology makes sense except in the light of evolution.
>
> Dobzhansky (1964)

> Sadly, it's much easier to create a desert than a forest.
>
> James Lovelock

1.1 General introduction

Deserts are defined by their arid conditions. A consequence of this aridity is that most of the area occupied by desert is barren and monotonous, leading many people to view it as a wasteland. In contrast, biologists have long seen deserts as laboratories of nature, where natural selection is exposed at its most extreme. Generations of scientists have focused on the numerous unique adaptations of plants and animals for surviving the harsh desert environment. Indeed, such studies have made the adaptations of desert organisms some of the best-known examples of Darwinian natural selection. In this book, I will introduce the reader to the major constraints facing organisms in desert environments and also consider how organisms have evolved to circumvent these constraints. In this edition, I shall also stress the potential, and current, effects of global climate changes on desert environments. The effects of climate changes are likely to be most extreme in deserts and on their peripheries (Noble and Gitay 1996; Safriel et al. 2005; Shachak et al. 2006; IPCC 2013).

Researchers are also very interested in the biotic interactions among desert organisms. I will attempt to convince the reader that, while the abiotic environment defines deserts and imposes strong selection pressure on the organisms that live there, the biotic interactions among the organisms in deserts are no less exciting or intricate than those of other environments. Indeed, it is the relative simplicity of desert ecosystems that makes them more tractable for study than more complex environments. I will also emphasize the myriad ways in which organisms exploit the enormous spatial and temporal variations in deserts, leading to the creation of unique assemblages with surprisingly high diversity.

Finally, the book will examine the sensitivity of the desert environment to disturbances and the effects that human beings have had on deserts. It will focus on the

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paradox that deserts have been particularly important habitats for humans despite their aridity and how changing resource use patterns are placing these unique ecosystems under threat. In particular, I will consider the serious negative consequences our use of the environment is having on deserts.

1.2 What creates a desert?

Deserts are defined by their aridity, yet differ enormously in their abiotic characteristics. The variation among deserts is probably greater than for any other biome, largely because deserts are so widely spaced on the planet and have arisen for very different reasons. For example, North American continental deserts are far hotter in the summer (Thomey et al. 2014) and wetter than African and Middle Eastern deserts (Peel et al. 2007). The Kalahari (Plate 1) and Namib deserts (Plate 2) in southern Africa mostly experience summer rainfall and are dominated by grasses, while the adjacent succulent Karoo Desert experiences winter rainfall and is dominated by succulents (Mucina and Rutherford 2006). In contrast, Middle Eastern deserts experience winter rainfall and are dominated by annual forbs (mostly Asteraceae). The coastal Namibian and Chilean desert systems are driven by fog (Ebner et al. 2011; Amundson et al. 2012), while run-off from winter floods controls plant production in Middle Eastern deserts (Bruins and Ore 2009). Australian deserts (Plate 3) are limited by phosphorus (Orians and Milewski 2007), while nitrogen is the most limiting nutrient in other deserts (Schlesinger and Pilmanis 1998; Ezcurra 2006). An additional classification is that of drylands (Safriel et al. 2005; Shachak et al. 2006). Drylands are regions where precipitation is counterbalanced by evaporation from surfaces and transpiration by plants (= evapotranspiration) (see 'Aridity indices' later in this chapter). The drylands can be further classified into four subtypes: dry subhumid lands, semi-arid lands, arid lands, and hyperarid lands. Usually, hyperarid lands and even arid lands are not considered drylands (Stafford Smith and Cribb 2009).

1.3 Deserts have low precipitation and high variability in precipitation

It is critical to consider deserts both as resource-poor environments and as places where there are enormous variations in environmental quality in space and time. Ward et al. (2000a) have shown that there is a strong negative correlation between the coefficient of variation (c.v.) in annual rainfall and its median value in arid systems (Figs. 1.1a and b). Le Houérou (1984) noted that in the north of the Sahara, the c.v. of annual rainfall increased from 25–30% in the 400- to 500-mm zone to 70–80% in the 100-mm belt. In a study on North American deserts, Davidowitz (2002) has shown that this trend is generally true there as well. Coefficients of variation of mean annual rainfall in specific places may be as much as five times higher than in mesic places. However, Davidowitz (2002) warns that this is not universally true. Indeed, there may be places in North America where there is no difference in c.v. between xeric and mesic sites. Nonetheless, this variation in environmental quality leads to high local species diversity and allows deserts to be exploited by a wide variety of organisms that are more common in mesic environments (see Chapters 3, 4, and 8). Another useful measure is seasonality of rainfall. Fisher (1994) suggests that one should use the 12-month autocorrelation coefficient (Fig. 1.2). High autocorrelation functions at 1- or 2-month time lags indicate seasonality over short time periods (1 or 2 months). An additional factor that may be important is the magnitude of rain events (Stafford Smith and Cribb 2009) (Fig. 1.3). Unlike humid areas where rain may fall continuously for several days at a time, rain in deserts falls in discrete events (Ezcurra 2006).

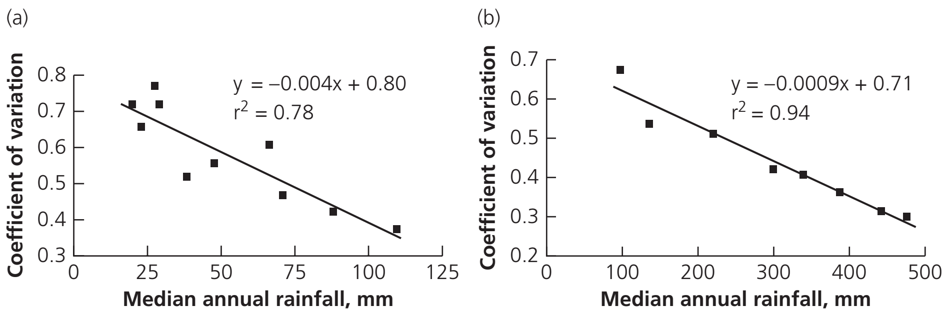

Fig. 1.1 Strong negative correlation between the coefficient of variation (c.v.) in annual rainfall and its median value. (a) Negev Desert, Israel. (b) Namib Desert, Namibia.

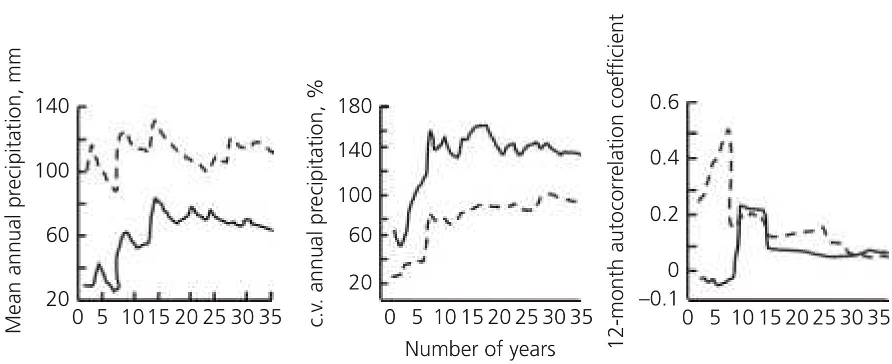

Fig. 1.2 The 12-month autocorrelation coefficient of total monthly rainfall for two sites in Oman. Dashed line = Salalah; solid line = Masirah. The higher autocorrelation coefficient for Salalah indicates a briefer season than for Masirah.

Source: From Fisher (1994). With kind permission of John Wiley and Sons.

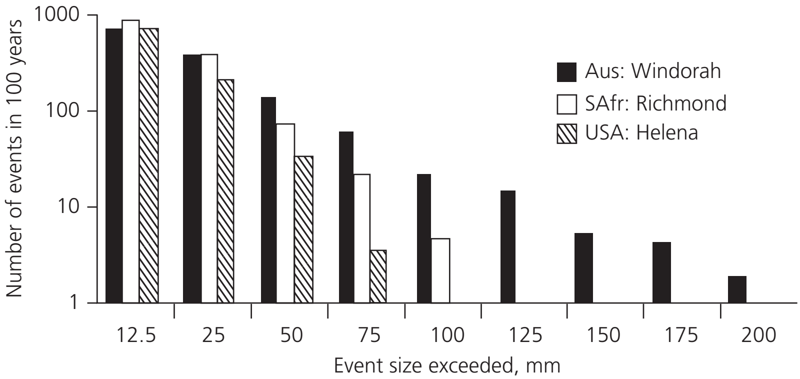

Fig. 1.3 Australian rainfall stations have many more, and much larger, rainfall events than arid South African sites, which, in turn, have more than those in the arid parts of the U.S.A. The histogram compares the size of rainfall events over 100 years at three weather stations with roughly the same seasonality and average annual rainfall (all about 300 mm yr^{-1} with about 2/3 in summer)—Windorah in western Queensland in Australia, Richmond in the Northern Cape in South Africa, and Helena, Washington, U.S.A. There are many events of at least 12.5 and 25 mm at all stations, but only Windorah in Australia has events > 125 mm, and its extremes are sometimes larger than 200 mm.

Source: From Stafford Smith and Cribb (2009). With kind permission of CSIRO Publishing.

1.4 How old are deserts?

One may be tempted to assume that deserts have always been so. However, fossils found in deserts such as those discovered in the Gobi Desert of China (Plate 4) by Roy Chapman Andrews in the 1920s as well as many subsequent discoveries in Chinese deserts (e.g. Liu et al. 2002; Sereno 2011), the *Lystrosaurus* fossils in the Karoo Desert (Botha and Smith 2007), the ammonite fossils in the Arabian and Egyptian deserts (Plate 5) (Radner 2007; Nagm and Wilmsen 2012), and the soft-bodied Ediacaran fossils of the Great Basin Desert (Hagadorn and Waggoner 2000; Jensen et al. 2006) and fossil (aquatic) foraminifera in Australia (Cann and De Deckker 1981) indicate that these were once shallow seas, deltas, or even, in the case of the Arabian desert, areas of the former Tethys Sea when the world was a single continent known as Pangaea (Golonka and Bocharova 2000; Scotese 2004). Plate tectonics has resulted in major changes in the positions of the continents and, consequently, in the positions of the deserts (Wegener 1966).

Many, if not most, deserts are reasonably young, although they do vary considerably in age, persistence through geological time, and the types of habitats occurring on their borders. This, in turn, affects the types of flora and fauna that deserts are likely to attract (Kelt et al. 1996; Soykan et al. 2012). It is generally agreed that the Miocene (23.5 million to 20,000 years BP) was a time of global desertification (Axelrod 1950; Alpers and Brimhall 1988; Singh 1988; Dunai et al. 2005; Bristow et al. 2007; Zhang et al. 2014).

The deserts of central Asia (Gobi, Taklamakan, Turkestan) are considered old Cretaceous (144–58 million years BP), although they were not widespread until the Miocene (Sinitzin 1962). The exception in this region is the Thar Desert of India, where most sand landscapes were developed due to human activities in historical times (Wadia 1960; Prakash 1963). The Taklamakan Desert in southern China formed about 5 million years ago (Sun and Liu 2006). The permafrost (permanently frozen ground) in the Gobi Desert is much more recent (Owen et al. 1998), being only about 15,000–22,000 years old.

Australian deserts have only been arid for about a million years at most (Ollier 2005), and perhaps only experienced a sharp increase in aridity about 350,000 years ago (Hesse et al. 2004). The Atacama Desert in South America (Plate 6) is about 25 million years old at the oldest (Dunai et al. 2005), although estimates indicate that about 10–15 million years old may be more appropriate (Prellwitz et al. 2006). Also in South America, the Patagonian Desert is about 25 million years old (Dunai et al. 2005).

Although the Sahara (Plate 7) is the largest desert in the world (about 9 million km^2), it was formed about 7 million years ago (Schuster et al. 2006; Zhang et al. 2014); some claim that it only became desert about 2–3 million years ago (Kroepelin 2006; Kröpelin et al. 2008). Zhang et al. (2014) claim that the closing of the Tethys Sea (the forerunner of the modern Mediterranean Sea) as a result of the shifting of the African tectonic plate relative to the Eurasian plate was associated with the earlier aridification of the Sahara Desert, some 7 million years ago. The Namib Desert is believed by some to be the world's oldest desert. It is claimed to have been arid for at least 55 million years and, perhaps, as much as 80 million years BP (Ward et al. 1983). The current Namib Desert overlies the Tsondab sandstone, with very similar geology to the current desert, indicating that this desert has been arid for a very long time (Kocurek et al. 1999; Stone 2013). The convergence of the Benguela upwelling and the hot interior have maintained, and perhaps increased this aridity in recent times but they did not generate the aridity. The region, isolated between the ocean and the escarpment, is considered to be a constant island of aridity surrounded by a sea of climatic change (Ward et al. 1983; Armstrong 1990; Goudie 2010). The arid conditions probably started with the continental split of West Gondwana 130–145 million years ago when this area shifted to its present position along the Tropic of Capricorn (Ward et al. 1983). This lengthy dry period has had a profound influence on the region's biodiversity. The region has remained a relatively stable centre for the evolution of desert species. This has resulted in a unique array of biodiversity with high levels of endemism and numerous adaptations to arid conditions (Crowe and Crowe 1982; Barnard et al. 1998; Lamb and Bond 2013), and may explain why so few species are shared between the Namib and the Sahara (Crowe and Crowe 1982; Shmida 1985) (see Chapter 9).

1.5 Deserts are created by a lack of precipitation and not high temperatures

What makes a desert is not a particular temperature but rather a lack of precipitation. The Arctic and Antarctic polar regions (Plate 8) have large barren stretches that can be considered desert (Priscu et al. 1998). Similarly, the Great Basin Desert does not have the extreme temperatures of the Sonoran Desert or the Sahara. Most deserts lie in two belts between the Equator and the tropics of Cancer and Capricorn. In the Northern Hemisphere, the arid belt includes the Sahara, Arabian, and Iranian deserts, the Gobi and central Asian deserts, and the deserts of the North American Southwest. In the Southern Hemisphere, the arid belt includes the Namib and Kalahari deserts, the deserts of Peru and Chile, and the Australian deserts (Fig. 1.4).

Until fairly recently, a desert was considered a place that received less than 250 mm of rainfall. If distributed evenly over the entire year, 250 mm of annual rainfall can be sufficient to maintain a grassland, yet when concentrated in 1 or 2 months, deserts may exist because plants can use only a certain amount of rain at a time. Rain that falls in torrents usually runs off or sinks into the ground before it can be used. Thus, flash floods can create far more than 250 mm of rainfall but they are not accessible to

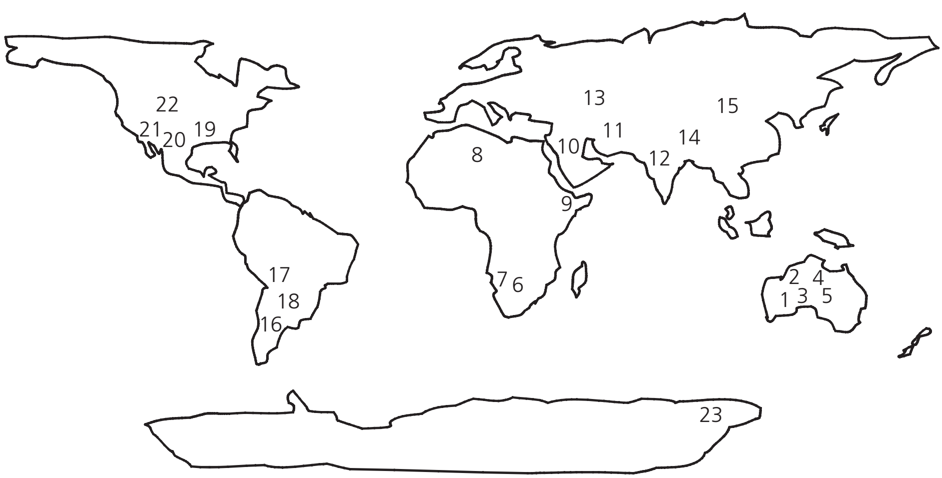

Fig. 1.4 Map of deserts of the world. Names of deserts: 1 = Victoria Desert; 2 = Great Sandy Desert; 3 = Gibson Desert; 4 = Simpson Desert; 5 = Sturt's Stony Desert; 6 = Kalahari Desert; 7 = Namib Desert; 8 = Sahara; 9 = Somali-Chalbi Desert (also known as the Ogaden Desert); 10 = Arabian Desert; 11 = Iranian desert; 12 = Thar Desert; 13 = Turkestan Desert; 14 = Taklamakan Desert; 15 = Gobi Desert; 16 = Patagonian Desert; 17 = Atacama-Sechura Desert; 18 = Monte Desert; 19 = Chihuahuan Desert; 20 = Sonoran Desert; 21 = Mojave Desert; 22 = Great Basin Desert; 23 = dry valleys of Antarctica (Plate 8).

Source: Modified from Page (1984).

desert organisms because most of the rainfall is not absorbed by the soil, leaving the ground nearly as dry as it was without rain. Furthermore, some deserts (deemed 'cold' deserts) receive precipitation as snow and ice, which can exceed the 250-mm threshold, but that precipitation is again not accessible to organisms. Here, I will include mean annual rainfall values up to 500 mm where appropriate to include regions that border on deserts but that are not grasslands or savannas. While the main deserts are indicated in Fig. 1.4, there are many smaller areas containing deserts (e.g. the Turkana Desert of Kenya and the Karoo of South Africa) that are not specifically illustrated. Indeed, deserts make up about 40% of the world's biomes (Ezcurra 2006).

1.6 Aridity indices

Rainfall alone is insufficient to describe desert conditions, so some scientists have devised systems that relate potential evaporation to precipitation (Thornthwaite 1948; Geiger 1961). Thus, in the Atacama and Namib deserts, two of the driest places on Earth, the sun's energy can evaporate 200 times as much rainfall as the area receives in an average year. The aridity index is thus 200 (Page 1984) and both areas are classified as 'hyperarid'. At the other end of the scale, the Great Basin Desert in North America has an index that ranges from 1.5 to 4. This region is known as 'semi-arid' and can support a wide diversity of life forms.

At the beginning of the twentieth century, Köppen (1931; modified by Geiger 1961) developed a concept of climate classification where arid zones were defined as areas where annual rainfall (in cm) is less than $R/2$, where

$$R = 2 \times T \text{ if rainfall is in the cold season,}$$
$$R = 2 \times T + 14 \text{ if rainfall occurs throughout the year, and}$$
$$R = 2 \times T + 28 \text{ if rainfall occurs in summer,}$$

with T = mean annual temperature (in °C).

This was one of the first attempts at defining aridity that shows the effects of the thermal regime and the amount and distribution of precipitation in determining the native vegetation in a particular area. It also recognized the significance of temperature in allowing colder places such as northern Canada to be recorded as humid despite having the same precipitation as subtropical deserts because of the lower potential evapotranspiration in colder places. In the subtropics, the difference between rain falling in warm and cold seasons recognizes the greater potential impact of rain in winter because of its effects on plant growth. Athens, Greece (mean annual rainfall = 372 mm), receives most of its rainfall in winter and is considered to have a humid climate with roughly the same rainfall as semi-arid Kimberley, South Africa (mean annual rainfall = 390 mm), where most rain occurs in the hot summer. The most frequently used climate classification map of Köppen (1931) was presented in its latest version by Geiger (1961) (Fig. 1.5) for the second half of the twentieth century.

Peel et al. (2007) further differentiated the Köppen–Geiger scheme (Fig. 1.5). They also distinguished hot deserts from cold deserts using three isotherms: a mean

Fig. 1.5 Climate classification map of Wladimir Köppen (1931) was presented in its latest version by Rudolf Geiger (1961). Black = extremely arid; Grey = arid to semi-arid.

Source: Modified from Peel et al. (2007).

annual temperature of 18°C, or a mean temperature of 0 or -3°C in the coldest month. A location with a climate with the appropriate temperature above whichever isotherm is being used is classified as 'hot arid', and a location with the appropriate temperature below the given isotherm is classified as 'cold arid'.

A more widely used index of aridity was developed by Thornthwaite (1948) as $AI_T = 100 \times d/n$, where the water deficiency *d* is the sum of the monthly differences between precipitation and potential evapotranspiration for those months when normal precipitation is less than normal evapotranspiration and *n* is the sum of monthly values of potential evapotranspiration for the deficient months (later modified by Huschke 1959).

A number of other aridity indices have since been developed. The United Nations Environment Programme (1992) defined aridity as $AI_U = P/PET$, where P refers to precipitation and PET refers to potential evapotranspiration. PET and P must be expressed using the same unit (e.g. in mm), and the resulting index is therefore dimensionless. Table 1.1 indicates the boundaries of hyperarid, arid, semi-arid, and dry subhumid and the percentage land area of the Earth that they occupy. Drylands

Table 1.1 Classification of deserts according to their level of aridity, following the scheme of United Nations Environment Programme (1992)

Classification	Aridity index	Global land area (%)
Hyperarid	AI < 0.05	7.5
Arid	0.05 < AI < 0.20	12.1
Semi-arid	0.20 < AI < 0.50	17.7
Dry subhumid	0.50 < AI < 0.65	9.9

The last column indicates the percentage of land area currently occupied by these various categories. AI = aridity index. Drylands would be included in all areas with AI < 0.65 (Safriel et al. 2005), while deserts are often classified as areas with AI < 0.5 (Stafford Smith and Cribb 2009).

are considered to be tropical and temperate areas where there is an aridity index <0.65 (Safriel et al. 2005). Drylands even occur in certain areas of southern Europe, such as Spain and Greece. Deserts are defined as areas with an aridity index <0.5 and include semi-arid ecosystems (Stafford Smith and Cribb 2009) (Table 1.1).

1.7 What denies rainfall to deserts?

Four factors influence the lack of rainfall in deserts (Page 1984; Milich 1997):

1. The most constant of these is the global circulation of the atmosphere, which maintains twin belts of dry, high-pressure air over the fringes of the tropics, known as Hadley cells (Persson 2006). Air is fluid (Vogel 1994) and is kept in continuous motion by solar energy. When the sun's radiation reaches the earth, most passing through the atmosphere, it is absorbed by land and water and is then re-radiated as heat. Most solar radiation is absorbed in the tropics, where the sun is virtually directly overhead in summer and winter. As tropical air warms, it expands, becoming lighter than the surrounding air and rises, carrying with it huge volumes of water vapour from the warm ocean surface. As the moist air rises, it cools and spreads laterally, northwards and southwards. The cooling reduces its capacity to hold water and moisture begins to condense and fall in huge torrents of tropical rain. After further cooling and having been stripped of its water content, the increasingly heavy air sinks as it travels towards the poles and is compressed by the continuing flow of sinking air. This compression causes the air to warm again. This warm, dry, high-pressure air mass presses down at the tropics and then much of it flows back to the Equator into the low-pressure void left by the rising tropical air. The deserts of the subtropics are where the high-pressure air descends.
2. Circulation patterns in the sea also contribute to aridity when cold coastal waters (on the west coasts of North America, South America, and Africa) chill the air, reducing its moisture-carrying capacity. Prevailing winds blowing along the coastline tend, because of the Earth's rotation, to push surface currents seawards perpendicular to the wind. Because there is no surface water upcurrent to replace the water being driven out to sea, very cold water is drawn upward from near the ocean floor. This vertical movement of the ocean is known as an upwelling (Fig. 1.6). Air masses crossing these stretches of very cold water are chilled and their capacities to hold water vapour are diminished. The condensing moisture forms dense fog banks along the coast, leaving little or no rain to fall on the land. The Atacama and Namib deserts are largely formed by these processes (Armstrong 1990; Stone 2013). Some parts of these deserts can go for years without rain, although abrupt changes in the upwelling area (known as El Niño effect, which occurs in the Pacific Ocean off South America) can cause the trade winds to change and warm water to surge shoreward (Rasmusson and Carpenter 1982). This can cause heavy rain to fall. For example, in 1934, about 800 mm of rain fell at Walvis Bay in the Namib Desert, even though the mean annual rainfall there is 11 mm (Ward et al. 1998).

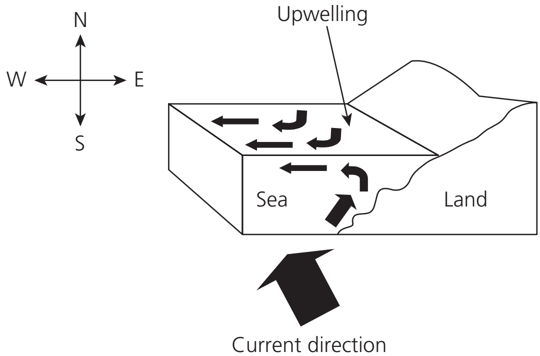

Fig. 1.6 A fog desert is created by vertical movement of the ocean known as an upwelling, which chills the air. These deserts usually form on the west coasts of southern continents.

Source: Following Ezcurra (2006). With kind permission of United Nations Environment Programme.

3. Even moisture-laden winds may not be able to carry rain if it is in a rain shadow (also known as *relief* desert) created by a mountain range (Fig. 1.7). The Great Basin Desert and the deserts of Afghanistan and Turkestan are examples of deserts created by this process.
4. If the distance to the interior of a continent is too great (e.g. China's Taklamakan and Gobi deserts) then water is limited. By the time that westerly winds have blown across central Asia, the winds would have travelled over thousands of kilometres of land and, hence, would have lost most of their moisture.

Many of these factors may work in tandem to create deserts (Table 1.2).

Arid lands are not entirely restricted to the subtropics. There are very cold deserts in China (Taklamakan and Gobi deserts), Turkmenistan and Kazakhstan (Turkestan desert), and the southern tip of South America (Patagonian Desert). The Great Basin Desert is also very cold in the winter. Relatively warm air at about 60°N and 60°S rises and flows towards the poles. As this air cools, it releases little moisture as rain or, more frequently, as snow. It then sinks and moves outwards to complete the circular flow (which is known as a Hadley cell—Persson 2006).

At the poles, there are regions that can also be classified as deserts by virtue of their low precipitation. They seldom receive more than 75–100 mm of precipitation and less than 120 mm of rain (Bockheim 2002; Pointing et al. 2009; Levy et al. 2011). Within the Arctic and Antarctic circles, there are barrens, which are ice-free rocks or sediments deposited by glaciers and where weak snowfalls are swept away by fierce winds. Parts of northern Greenland, the northern slope of Alaska, some northern Canadian islands, and a section of Antarctica also fall into this category. The cold that characterizes these polar barrens produces permafrost, which may extend as far below the surface as 300 m. When there is an annual cycle of freezing and thawing,

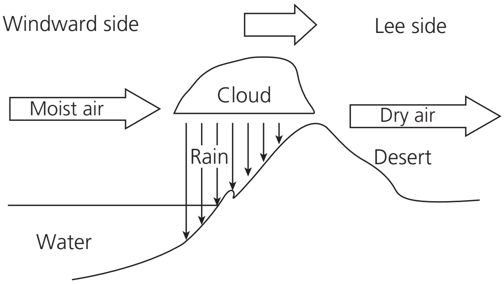

Fig. 1.7 A schematic diagram of a rain shadow desert.

Table 1.2 Reasons for the formation of deserts across the world

Continent	Desert	High pressure	Midcontinent	Rain shadow	Upwelling
Australia	Sturt's Stony	X	X	X	
	Victoria	X	X		
	Gibson	X	X	X	
	Simpson	X	X	X	
	Great Sandy	X	X		
Asia	Gobi		X		
	Taklamakan		X		
	Thar	X			
	Iranian	X	X	X	
	Turkestan		X		
	Arabian	X			
Africa	Somali-Chalbi	X			
	Kalahari	X			
	Namib	X			X
	Karoo	X		X	
	Sahara	X			X
South America	Patagonian			X	
	Monte	X			
	Atacama-Sechura	X			X
North America	Chihuahuan	X			
	Sonoran	X			
	Mojave	X		X	
	Great Basin			X	
Poles	Antarctic	X			
	Arctic	X			

this permafrost may be overlain by an active layer that, when it thaws in summer, may create pools. Among the more interesting of these polar deserts are the ice-free McMurdo Dry Valleys of Antarctica, near the Ross Sea (Gooseff et al. 2003). Aeolian distribution of organic material is thought to be a major source of nutrients for organisms inhabiting these valleys (Sabacka et al. 2012), aided by katabatic winds (also known as drainage winds) that carry high-density air from higher elevations down slopes by means of gravity. Most of the organisms inhabiting such dry, cold habitats are micro-organisms (Priscu et al. 1998), including four clades of cyanobacteria. In turn, these micro-organisms support invertebrate communities, including rotifers, tardigrades, and nematodes (Gooseff et al. 2003).

1.8 Global change and deserts

There are many studies that indicate that the size of deserts will increase with the global climate changes that are predicted (e.g. Volder et al. 2010; Engelbrecht and Engelbrecht 2016). This is largely due to increases in global temperatures (known as 'global warming') resulting from burning fossil fuels and industrial pollution. Bates et al. (2008) predict that globally averaged surface temperatures may rise by between 1.1 and 6.5°C, with higher values expected in deserts than the global average, resulting in an increase in the areas of these deserts. For example, Engelbrecht and Engelbrecht (2016) predict that the hot deserts of southern Africa will increase in area from 33.1% to 47.3–59.7% and the hot steppe zones will increase from 19.4% to 24.9–29.9% in a southerly and easterly direction. This global warming is likely to have effects that are greater than simply making hot deserts hotter. Global warming should cause intensification of precipitation events (Groisman and Knight 2008), which may result in more runoff from saturated soils and greater evaporation due to warmer ambient temperatures (Volder et al. 2010). In turn, this will cause an increase in the frequency, duration, and intensity of droughts (Fay et al. 2003). Another issue is that increasing temperatures lead to the loss of nitrogen, considered the most important nutrient for plant growth, from the soil (Tilman 1983; Reich et al. 2001; Reich 2009). Heat prevents microbes from converting nutrients to nitrates, which are necessary for almost all living things. This can reduce the already limited plant life in deserts.

Coupled with global warming is the increase in greenhouse gas concentrations, including global CO_2 levels (Wilkinson 2006; IPCC 2013) (Fig. 1.8). The atmospheric concentrations of the greenhouse gases carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) exceed the range of concentrations recorded in ancient ice cores. The past changes in atmospheric greenhouse gas concentrations are determined with very high confidence from these polar ice cores that are up to 800,000 years old (IPCC 2013). Carbon dioxide increases may have large effects on deserts. Elevated CO_2 will have a stimulatory effect on photosynthesis and growth. However, this will differ among plant functional types, particularly between three-carbon (C_3) and four-carbon (C_4) photosynthetic functional types (Wolfe and Erickson 1993; Ward 2010) (Fig. 1.9). There are likely to be changes in the dominance of plants that use C_3 photosynthesis over plants that use C_4 photosynthesis (Bond and Midgley

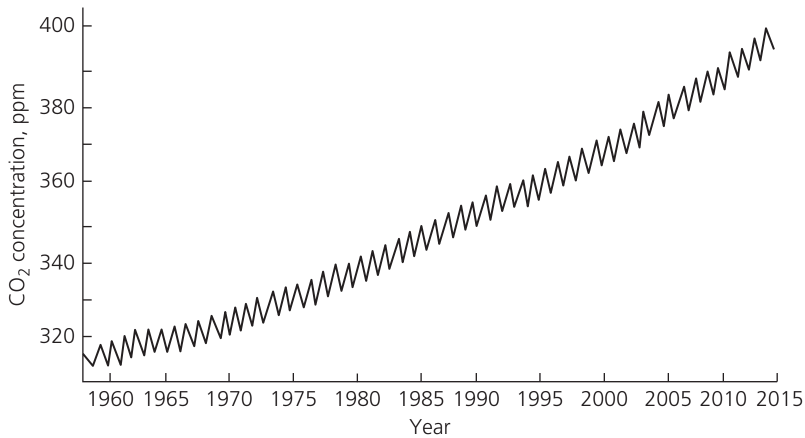

Fig. 1.8 Carbon dioxide levels from Mauna Loa observatory, Hawai'i, U.S.A.

Source: From N.A.S.A.

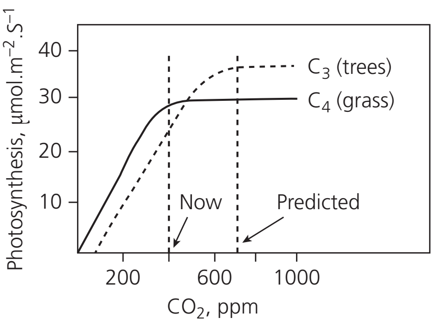

Fig. 1.9 Net photosynthetic rates differ between C_3 and C_4 photosynthetic functional types at different CO_2 concentrations.

Source: Modified from Wolfe and Erickson (1993) and Ward (2010). With kind permission of Springer.

2000; Ward 2010). C_4 plants are often known as warm-season plants because they are photosynthetically more effective than C_3 plants at high temperatures. However, C_3 plants are often woody and reduce the palatability of vegetation to herbivores (both wild and domestic) (Ward 2010).

Methane is most often produced as a by-product of digestion by ruminant herbivores (such as domestic livestock), rotting plant materials, and degradation in landfills. Thus, because relatively few people and their livestock live in deserts, this is considered to be less of a problem in these environments (Safriel et al. 2005). Similarly, nitrous oxide (N_2O) is largely a by-product of industrial production and is not usually considered to be a desert-specific issue (although see Xu-Ri et al. (2003) for a counter-example from Mongolian desert grasslands).

2 Abiotic Factors

Abiotic factors are the primary reason for the differentiation of deserts from other ecosystems. Fundamentally, it is the low rainfall that deserts experience that differentiate them from other habitats. Furthermore, deserts are broadly classified into hot and cold deserts. Frequently cold deserts occur at high altitudes, such as the Tibetan Plateau. Similarly, there are areas of the Arctic and the Antarctic that receive very little rainfall and are very cold. I also consider the role of geology, particularly in terms of the effects on soils, which in turn is important for plant life and to a certain extent animal life (e.g. those animals living in burrows). The last abiotic issue that I cover is fire. As this book focuses on the biology of deserts, there will be some issues that I will not cover, but I believe that sufficient knowledge will be gained to serve for the understanding of subsequent chapters.

2.1 Precipitation

2.1.1 Rainfall

It is widely known that deserts are defined by their low mean rainfall, although it is just as important to measure the temporal variability in annual rainfall (see Fig. 1.1). Similarly, spatial variation in rainfall is high. For example, Sharon (1972) has shown that the correlation coefficient for rain gauges in the Negev Desert (Israel) may vary from 0.95 at distances less than 1 km to as little as 0.15 at distances greater than 23 km apart (Fig. 2.1). In the Namib Desert, Sharon (1981) has also shown that there are weak correlations between rain gauges with increasing distance. He found that convective storms are not randomly scattered in space, but rather tend to cluster at distances of 40–50 km and 80–100 km from one another, with no preferred locations of, or directions between, storms. It is this high variability that leads to the high biodiversity that occurs in some desert areas. For example, α diversity of plants (diversity in a particular place) in Middle Eastern deserts (Naveh and Whittaker 1979; Ward and Olsvig-Whittaker 1993) is several times higher than that of the world's richest plant kingdom, the Cape Floral Kingdom of South Africa (Cowling 1992).

Rainfall in deserts tends to fall in pulses (Austin et al. 2004; Liu et al. 2013; Collins et al. 2014). These pulses can vary considerably in their magnitude and timing. They can fall in summer or in winter and can vary considerably in the amount of rain

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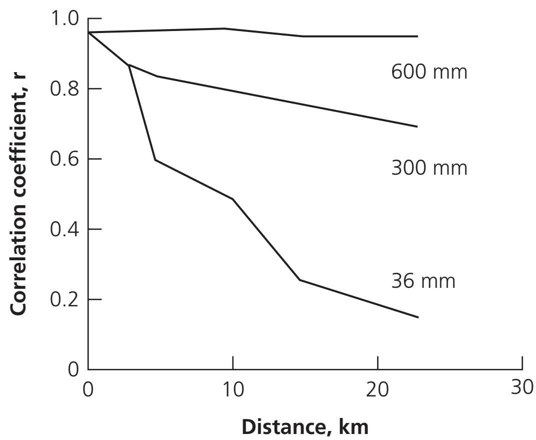

Fig. 2.1 Spatial variation in rainfall in desert (36 mm), semi-arid (300 mm), and mesic (600 mm) areas. Correlation coefficients are based on daily rainfall variation over 3 years.

Source: Modified from Sharon (1972.)

that falls. Short precipitation pulses may be sufficient for annual plants but perennial plants need far longer periods of rain for effective growth (Ivans et al. 2003). Pulses may be local in scale but are, nonetheless, driven by large-scale global and atmospheric factors such as the position of the jet stream, polar boundary shifts, El Niño-Southern Oscillation events, and even longer-term ocean cycles (Nano and Pavey 2013).

The erosion and scouring effects of torrential downpours can be marked in desert landscapes. In sandy deserts, rain usually drains away and changes in the landscape are reasonably small. In contrast, downpours in rocky deserts drain rapidly into adjacent *wadis* (Arabic; also known as *arroyos* in Spanish), which are ephemeral rivers (Fig. 2.2). These wadis can be heavily affected by downpours, and they frequently are subjected to flash floods because there is little or no vegetation to hold the water back. Such flash floods carry sand and gravel and later rocks and boulders with them, adding to the erosive power of water as it rushes down the slope. This is known as the threshold of critical power, which is the power needed to cause water to flow (Bull 1981; Tucker and Slingerland 1997) (Figs. 2.3 and 2.4). At the end of most wadis lies an alluvial fan (called a *bajada* in Spanish) (Fig. 2.5) made up of sand and stone. At this point, the critical power threshold (Bull 1981) is no longer exceeded as the water moves into a more open landscape. The torrent subsides and most of the sand, stone, and boulder contents are dropped into the alluvial fan (McAuliffe 1994). The substrate is coarser, with larger rocks on the upper bajada and finer stones and gravel at the lower elevations (McAuliffe 1994). The water may pass into a *playa*, which is a water body with no exit. During wet cycles, shallow playa lakes may last for a few months, a few years, or even longer. Some playa lakes may last for considerably longer; for example, the Salton Sea, in California (U.S.A.), has been present since 1906 (King et al. 2011).

Fig. 2.2 Augrabies waterfall in the arid Northern Cape province, South Africa. The Orange River runs through here, dropping over 190 m en route to the sea.

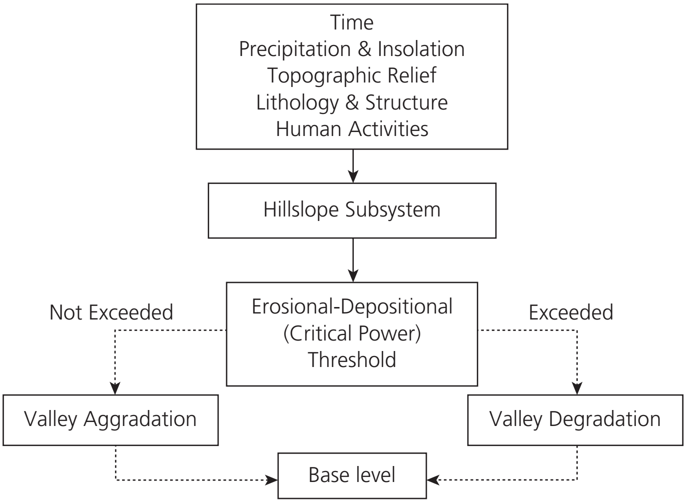

Fig. 2.3 Basic elements of a fluvial system. Feedback mechanisms are indicated by dashed lines and arrows.

Source: From Bull (1979). With kind permission of the Geological Society of America.

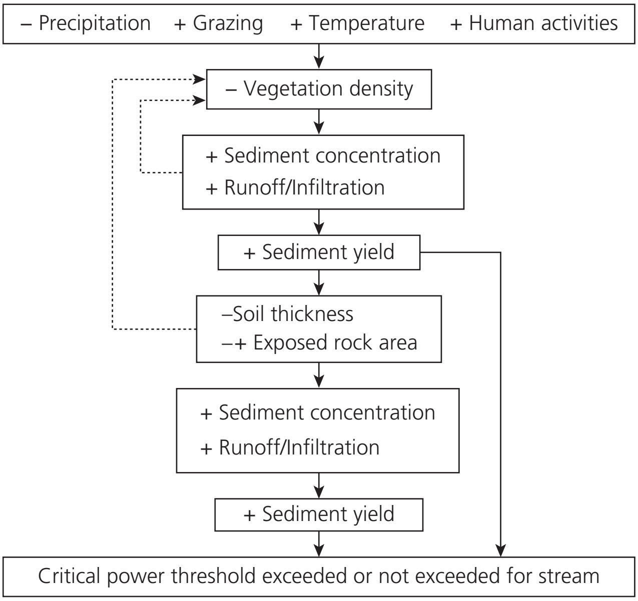

Fig. 2.4 Increases (+) and decreases (–) in elements of an arid hillslope subsystem. Self-enhancing feedback mechanisms are shown by dashed lines.

Source: From Bull (1979). With kind permission of the Geological Society of America.

Fig. 2.5 Satellite view of an alluvial fan in the Taklamakan Desert in Xinjiang, China. This alluvial fan is 60 km long and stretches across the landscape between the Kunlun and Altun mountain ranges that form the southern border of the Taklamakan Desert. Most alluvial fans are not nearly as long as this.

Source: Photo: NASA/GSFC/METI/ERSDAC/ JAROS, and U.S./Japan ASTER Science Team.

One of the most interesting phenomena regarding playas is the observation that large, heavy objects such as stones, rocks (Fig. 2.6a), and even bones (Fig. 2.6b) move on them (Lorenz et al. 2011; Norris et al. 2014; Baumgardner and Shaffer 2015). The heaviest rock had a calculated weight of 320 kg (Sharp and Carey 1976). Early hypotheses suggested that powerful winds (e.g. Shelton 1953; Sharp 1960) or thick ice floating rocks off the playa surface (Kletetschka et al. 2013) were responsible for this movement. Jones and Hooke (2015) have recorded that wind alone is sufficient to move rocks on a water-slickened surface. However, Lorenz et al. (2011) and Norris et al. (2014) found that the process of rock movement usually occurs when thin, 3- to 6-mm ice sheets, covering the playa pool, begin to melt in late morning sun and break up under light winds of about 4–5 $m.s^{-1}$. Floating ice panels that are tens of metres in size push rocks at low speeds of about 2–5 $m.min^{-1}$ on trajectories determined by the direction and velocity of the wind as well as that of the water flowing under the ice. Baumgardner and Shaffer (2015) found that bones of cattle could also be moved considerable distances by a similar process. In arid Spain, Sanz-Montero and Rodriguez-Aranda (2013) found that microbial mats were responsible for moving stones and rocks on playas (Fig. 2.7). Microbial mats that are poorly attached to the substrate act as starting points of these stone and rock tracks. The flotation and transportation of the microbial upper layer by wind-generated water currents are suggested to be a critical element promoting the destabilization and subsequent transportation of the attached sediment, including the rocks. An additional factor, mentioned by Sanz-Montero and Rodriguez-Aranda (2013), is the sudden exposure of bubble-separated sediment as a source of buoyancy. This bubble-separated sediment may be necessary to initially lift the rocks and to reduce the friction on the base of the rocks. These authors found that the rocks and the sediment mounds often overlap at the end of the tracks, indicating that rocks were embedded and transported by sediment rafts across the surface of the playa.

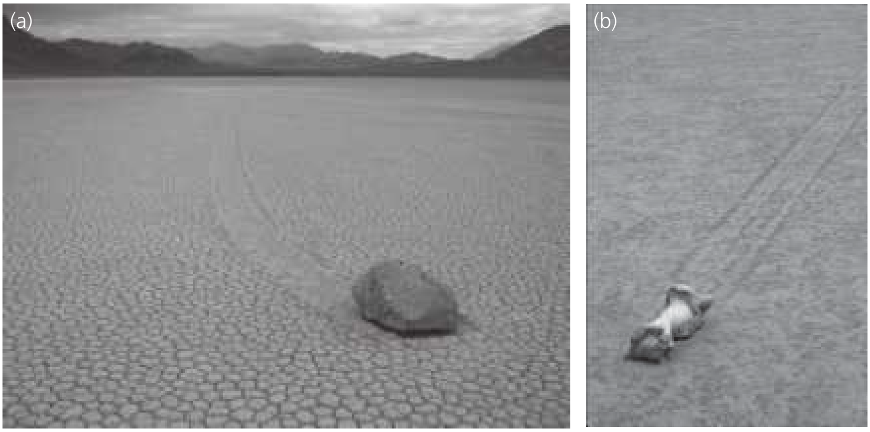

Fig. 2.6 Sliding rocks (a) and cattle bone (b) on playas.

Source: Photos from K. Lorenz, Johns Hopkins University Applied Physics Lab, Laurel, Maryland (a) and George Baumgardner, Nevada State Museum, Carson City, Nevada (b).

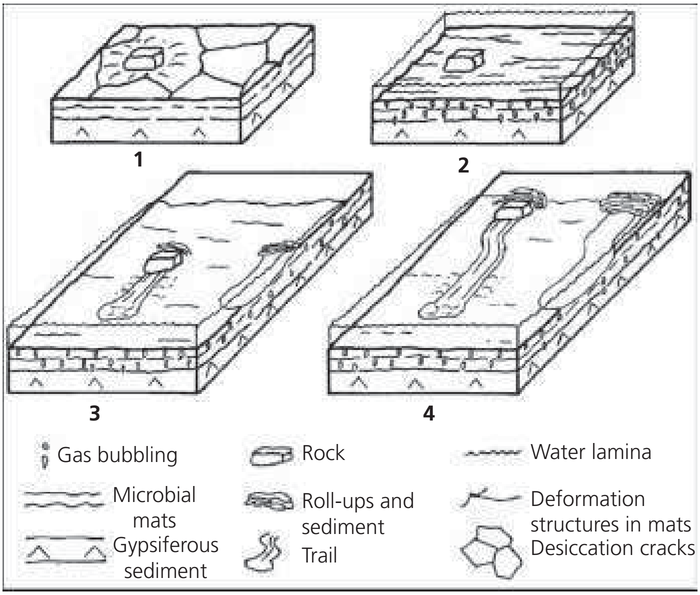

Fig. 2.7 Phases of track formation in the movement of rocks by microbial mats on playas. (1) A rock rests on a surface with desiccation cracks. (2) The playa is inundated with precipitation and microbial mats develop on the surface. Gases produced by micro-organisms may accumulate in bubbles below the upper mat, which favours its flotation. (3) Wind-induced water currents and traction cause the fragmentation and transportation of portions of the mat. The sudden exposure of the underlying bubble-separated sediment acts as a catalyst for the motion and transportation of sediment mounds and attached rocks. (4) The result is the trails that objects have left behind that end at the water's edge.

Source: From Sanz-Montero and Rodriguez-Aranda (2013). With kind permission of Elsevier.

In some areas, wadis may feed into rivers or lakes (e.g. Negev Desert wadis feed into the Dead Sea (Israel), some Sonoran Desert wadis feed into the Colorado River (U.S.A.), and Simpson Desert wadis feed into Lake Eyre (Australia)) or even into the ocean (e.g. Sonoran Desert wadis empty into the Pacific Ocean (Mexico) in certain areas). Poorly drained patches and larger playas may become alkaline (salty) through accumulation of soluble chemicals (see section 2.4.1.2, 'Saline soils').

2.1.1.1 El Niño-Southern Oscillation

The term 'El Niño' was originally applied to an annual weak warm ocean current that ran southward along the coast of Peru and Ecuador about Christmastime (25 December). This phenomenon only subsequently became associated with the unusually large warming of the ocean that occurs every few years (range = 2–7 years; mean = 5 years—Trenberth 1997) and changes the local and regional ecology. La Niña is associated with changes in wind direction off the coasts of

Peru and Ecuador. During La Niña conditions, the east to west flow present during neutral conditions is intensified and cooler conditions predominate. El Niño events tend to only last for a single cycle (i.e. one year from autumn to autumn), but it is not uncommon for multi-year La Niña events to occur. For example, the 1998–2001 La Niña affected three consecutive years from autumn 1998 to autumn 2001.

During El Niño conditions, the east to west winds weaken and an anomalous west to east wind predominates. Trenberth (1997) conducted a review of the term and found that an El Niño can be said to occur if 5-month running means of sea surface temperature (SST) anomalies in the El Niño region (5°N–5°S, 120°–170°W) exceed 0.4°C for 6 months or more. The interaction of the atmosphere and ocean is an essential part of El Niño and La Niña events. During an El Niño event, sea level pressure tends to be lower in the eastern Pacific and higher in the western Pacific while the opposite tends to occur during a La Niña event. This switch in atmospheric pressure between the eastern and western tropical Pacific is called the Southern Oscillation. El Niño and the Southern Oscillation are related and are usually combined as the El Niño-Southern Oscillation (ENSO).

The west to east flow of El Niño events drives warm equatorial waters from the western Pacific towards the eastern Pacific and northern South America. Indeed, this effect is felt across the entire Southern Hemisphere and can sometimes occur in the Northern Hemisphere (Polis et al. 1997). Among the most notable effects of El Niño are the droughts that it causes in the Southern Hemisphere (Stafford Smith and Cribb 2009) and the concomitant effects on the ecology and physiology of animals (e.g. Lovegrove 2000, 2003) and plants (Gutierrez et al. 2000; Gutierrez and Meserve 2003; Holmgren et al. 2006). However, there may also be positive effects; for example, the soil seed banks in the coastal Chilean desert are 5–10 times larger in El Niño years (Gutierrez et al. 2000; Gutierrez and Meserve 2003).

2.1.1.2 Oases

No desert is totally dry, although one may have to travel great distances to find water. Somewhere underground there is a continuous supply of flowing water. Its source is the rain that seldom falls, perhaps hundreds of kilometres away. A common source for an oasis is the rain that falls on the windward side of a mountain and soaks into a porous rock called an aquifer. This groundwater seeps down the tilted aquifer until it is stopped by an impermeable rock at a fault, where hydraulic pressure forces it to the surface. An oasis can also occur at a site where the erosive forces of wind and sand have created a basin lower than the elevation at which the rain fell (Goudie 2008). Water in the saturated portion of the aquifer flows along the sloping course until it intersects with the desert surface at what is called an artesian well (Land and Newton 2008; Garza et al. 2014). Certain artesian wells can be home to endemic aquatic organisms not found elsewhere (e.g. Guzik et al. 2012).

Oases can also be saline (Fan et al. 2008). If the water moves slowly through an aquifer it may leach out large amounts of salt from the rock (Walvoord et al. 2002). Only a few plants can survive in the marshes surrounding these salty springs (Arndt et al. 2004). Narrow oases can also form along rivers such as the Nile River in Africa and the Rio Grande and Colorado River in North America. These rivers form in tropical (e.g. Nile) or temperate regions (e.g. Colorado).

2.1.1.3 Fog

Some deserts are coastal (e.g. Namib (Namibia), Atacama (Chile and Peru), western part of the Sahara and Baja California section of the Sonoran deserts) and, although rainfall is very low, fog coming off the sea is sufficient to drive these systems. The Atacama Desert is considered to be the driest desert in the world, and it has been claimed that it did not receive any rain from 1570 until 1971 (Cockell et al. 2008); however, this desert does receive fog as its main source of precipitation.

The high levels of fog moisture in coastal desert fog zones provide habitats extremely favourable for lichen growth (Belnap et al. 2013). Much of this moisture is unavailable to vascular plants, allowing a large biomass of lichens (Fig. 2.8) to occur in areas with little or no vascular plant cover.

2.1.1.4 Run-off

High run-off from desert slopes (Fig. 2.9) is another factor that leads to high spatial patchiness in some deserts, such that run-on areas (usually in wadis) may have sufficient water availability to maintain important crops. The importance of run-off in desert ecosystem function has been particularly well studied in the Middle East, where people (most notably, the Nabateans; Fig. 2.10) exploited its availability from as early as 300 BC (Avni et al. 2006, 2010). The Nabatean people grew grapes at the beginning of the Common Era (AD 0) in the Negev Desert (with a probable effective

Fig. 2.8 Foliose lichen, Namib Desert, Namibia.

Fig. 2.9 Hillslope system on a limestone hillside in the Negev Desert, Israel.

mean annual rainfall of about 400 mm; this is the minimum required to grow crops) under conditions that do not differ from today's conditions (mean annual rainfall of 90 mm) (Ore and Bruins 2012).

Howes and Abrahams (2003) have modelled run-off and run-on processes in a desert shrubland in the Chihuahuan Desert (North America). Run-on infiltration can supply between 3 and 20% of water flow to shrubs, while the remainder arrives by direct precipitation on the shrubs (Martinez-Meza and Whitford 1996). Shrubs often occur on microtopographic mounds a few centimetres high, which means that run-on infiltration will not occur unless the flow is sufficiently deep (Howes and Abrahams 2003). The most favourable conditions for run-on infiltration are an initially

Fig. 2.10 Ridges in the desert hillsides built by the Nabatean people (100 BC to AD 200) to effectively channel run-off to increase the amount of water collecting in the ephemeral water courses.

wet soil and low-intensity rainfall events. Run-on infiltration is generally more effective for shrubs that have grasses at their bases (see also Abrahams et al. 1995) than bare soils, because of the greater penetration of the soil by the dense matrix of roots that promote infiltration via the creation of macropores in the soil. Howes and Abrahams (2003) consider run-on infiltration to be ineffective in the summer months when rain falls because of monsoonal events from the Gulf of Mexico that saturate the surface of the soil. In the latter case, the rain passes by the shrubs and empties into the arroyos (wadis). Abrahams et al. (1995) have shown that the increased run-off (and erosion) can result in stripping of the surface soils, the formation of desert pavement (*reg*; see section 2.4.1.3, 'Stone') in intershrub areas, and the development of rills (small channels or streams, usually created by soil erosion) (see section 2.4, 'Geology').

2.2 Temperature

The effects of temperature in deserts are widely known. However, little emphasis has been placed on the large differences among deserts in ambient temperature (and seasonality) and how these differences affect the organisms that live there. As mentioned in Chapter 1, the central parts of North American deserts, for example, have far higher temperatures and evaporation than African and Middle Eastern deserts, leading to more extreme conditions.

2.2.1 Hot deserts

The highest air temperature ever recorded was 57°C in Azizia in the Libyan part of the Sahara in September 1922 (Page 1984). Temperatures on the soil surface can be considerably higher, as much as 75–80°C (Ward and Seely 1996a). However, the temperature of winter nights in these deserts may fall below freezing point and daytime maximal temperatures may exceed 40°C. The major deserts in this category include the Sahara, Namib, Kalahari, Arabian, Iranian, Sonoran, Mojave, Chihuahuan, and Australian deserts.

2.2.2 Cold deserts

Cold deserts have hot summers counterbalanced by relatively or extremely cold winters (Peel et al. 2007). For example, for half the year, the Gobi Desert lies below 0°C. In the arid parts of Antarctica, mean winter temperatures may be as low as -30°C, while, in summer, diurnal temperatures will exceed 5°C for only a few weeks (McKay et al. 2009). Most cold deserts lie in the Northern Hemisphere (with the exception of the Patagonian Desert) and away from the tropics, because only great distances from the ocean make them both hot in the summer and cold in the winter. The Patagonian Desert is the exception here because it does not occur far from the ocean. Rather, it is the fact that it is in a rain shadow and because it is relatively close to Antarctica that makes it so cold. Cold deserts include the Great Basin, Patagonian, Turkestan, and Gobi deserts (Page 1984; Flegg 1993).

2.3 Declines in pan evaporation

It is not only annual rainfall that makes deserts arid. It is also an effect of the ratio of evaporation to rainfall that is important. An effective index of evaporation commonly used at weather stations is a Class A evaporation pan (Fig. 2.11). This evaporation pan is a standard water-filled dish (1.2 m diameter and 0.25 m deep) and is the most widely used physical measure of the evaporative demand of the atmosphere worldwide (Lim et al. 2012). Analysis of global pan evaporation data has mostly recorded declines in evaporation (Roderick et al. 2009; Hoffman et al. 2011) despite the trend of rising global air temperatures (so-called 'global warming'); ordinarily one might have expected an increase in evaporation as global temperatures increased. This became known as the 'pan evaporation paradox' (Peterson et al. 1995; Brutsaert and Parlange 1998; Roderick and Farquhar 2002), because declines in evaporation occurred at the same time as global warming. Not all sites experienced declines in pan evaporation, however. For example, in the U.S.A., only 64% of sites with this type of pan evaporimeter experienced declines (Hobbins et al. 2004) while others experienced no change or increases. In semi-arid Israel, there was an increase in evaporation during the boreal summer months (Cohen et al. 2002) and no change in winter, ascribed in part to decreases in global irradiance and increases in water vapour pressure deficit and wind speed, the last-mentioned being associated with changes in wind direction. However, Roderick and Farquhar (2002) ascribed declines (not increases) in pan evaporation to declines in global irradiance.

Sites that have experienced declining pan evaporation are widely dispersed across the globe, including India (Chattopadhyay and Hulme 1997), the U.S.A. (Hobbins et al. 2004), Australia (Roderick and Farquhar 2002), China and the Tibetan Plateau (Liu et al. 2004; Zhang et al. 2007; Shen et al. 2010), former Soviet Union (Peterson

Fig. 2.11 Class A evaporation pan in the Namib Desert at the Gobabeb Research and Training Centre, Namib Desert, Namibia.

Source: Photo: Ruusa Gottlieb.

et al. 1995; Golubev et al. 2001), Iran (Tabari and Marofi 2011), and South Africa (Eamus and Palmer 2007; Hoffman et al. 2011). Roderick and Farquhar (2002) note that, despite the global increases in temperature, vapour pressure deficits (i.e. difference between water vapour at the ground surface and in the atmosphere receiving the water vapour) have often remained stable. Reduction in solar irradiance (so-called 'dimming') and wind speed (so-called 'stilling') appear to have been major causes of this phenomenon (Roderick et al. 2007). One of the earlier ideas proposed that, in water-limited environments, when the evaporation in the environment is high, the air over the pan would cool and humidity over the pan would rise, leading to reduced evaporation (Brutsaert and Parlange 1998). However, this would not explain a continuous decline, as has been reported in many cases. Also, not all sites reporting reduced evaporation are water-limited and yet they report similar declines. Wind speed may have a local effect because, as the local vegetation near the pan evaporimeter grows, winds would be reduced in speed, leading to reduced evaporation. This may also help explain why arid areas near oceans (e.g. in the Atacama Desert in Chile and the Succulent Karoo in the Western Cape in South Africa) experience increased pan evaporation with increasing wind speed while the reverse is true inland. Declines in solar radiation are due to an increase in cloud cover and aerosols and are consistent with observed increases in air pollution (Roderick and Farquhar 2002). Essentially, it is important to remember that pan evaporation is only an index of true (actual) evapotranspiration (incorporating *transpiration* as water loss from plants). Roderick et al. (2009) conclude that, in water-limited environments, the interpretation of declining pan evaporation is not straightforward because actual evaporation is controlled by supply (i.e. precipitation) and not demand. McMahon et al. (2012) sensibly point out that measurement of actual evapotranspiration requires knowledge of all of the key variables used to calculate actual evapotranspiration (temperature, precipitation, wind speed, radiation); otherwise, one assumes that one or more of these variables are not changing.

2.4 Geology

Many deserts have very high spatial variation in geological substrates and, consequently, soil type. Deserts can also have shifting habitats created by dune systems, which leads to the formation of unique vegetation forms and their associated fauna (Goudie and Seely 2011). Yet other deserts are highly saline (see below). Limestone deserts may support high densities of organisms, such as snails, otherwise associated with mesic ecosystems (e.g. in the Negev Desert) (Shachak et al. 1981).

As indicated earlier, plant productivity in deserts can be nutrient-limited. Nitrogen is the key limiting nutrient in most deserts (Jones and Shachak 1990; Schlesinger et al. 1990, 1996; Schlesinger and Pilmanis 1998; Cross and Schlesinger 1999), phosphorus is widely considered to be the most limiting nutrient in Australian deserts (Orians and Milewski 2007), while nitrogen, phosphorus, and potassium are limiting in sand dune communities in Africa's Namib and Kalahari deserts (Robinson

2001; Aranibar et al. 2004). In the Negev Desert of Israel, for example, nitrogen inputs are often low, soil nitrogen pools are small, and losses from run-off, erosion, volatilization, and denitrification can be high. Jones and Shachak (1990) have found an unusual but important source of soil nitrogen in the central Negev highlands of Israel, a limestone rock desert with patches of soil. Snails feed on endolithic lichens that grow within the rock, ingesting both rock and lichens, and depositing their faeces on the soil under the rocks. Snails transfer between 22 and 27 mg N m^{-2} per year to soil, which constitutes about 11% of total soil nitrogen inputs, at least 18% of net soil inputs, and a minimum of 27% of the nitrogen annually accumulated by endolithic lichens from dust.

In general, soil nutrients and organic matter tend to be concentrated in the upper 2–5 cm of the soil with the greatest amounts underneath the canopies of individual desert shrubs in 'islands of fertility' (Gonzalez-Polo and Austin 2009; Ravi et al. 2010). These resource islands harbour greater concentrations of water, soil nutrients, and micro-organisms than adjacent soils (Ravi et al. 2010). Moreover, the distribution of soil nitrogen, phosphorus, and potassium is strongly associated with the presence of shrubs in desert habitats because organic matter from the plants accumulates there (Aranibar et al. 2004; Ravi et al. 2010). The intershrub spaces are barren and comparatively devoid of biotic activity (Ravi et al. 2010).

Desert animals building their burrows in soil, such as isopods (which also consume soil), termites, ants, and rodents, change the chemical and physical qualities of the soil (including porosity, water-holding capacity, infiltration rates, redistribution of nutrients, and organic matter) and they can affect soil erosion and redeposition (Whitford 1999; Gabet et al. 2003; Whittington-Jones et al. 2011). For example, Shachak et al. (1976) have shown that the isopod *Hemilepistus reaumuri* in the Negev Desert highlands has an annual soil turnover of 28.5–105.7 g m^{-2}.

Thus, this variability in substrate type, while generally of lesser importance than rainfall and temperature, may play a key role in determining where desert organisms can live because rainfall and temperature vary relatively little within a particular area of a desert but substrates can vary considerably.

2.4.1 Desert landscapes

There are five major types of desert landscapes that are commonly recognized (Flegg 1993).

2.4.1.1 Sand

The sand desert landscape is not as common as is often perceived, and probably accounts for as little as 15–20% of deserts (Goudie 2010). The formation of sand dunes is an interesting process, nonetheless. Bagnold (1941) found that the wind must reach a particular speed before sand grains begin to roll along the surface. When a rolling grain encounters a stationary one, the collision may knock the other grain forward or propel it into the air. A fast-moving grain that strikes a pebble or another large obstacle may bounce into the air (Page 1984). However, the flight of any single sand grain is usually short-lived. Even in the worst sandstorms, individual grains seldom reach heights greater than 1 m. When the sand grain lands, it knocks other sand grains around. If the wind continues to blow, the air near the surface is soon filled with bouncing sand grains, with larger particles rolling along the ground. If a stream of moving sand encounters an obstruction, the air flow is disrupted. In front of the obstacle and to a larger degree just behind it, wind velocity drops and sand grains pile up (Bagnold 1941). The accumulation behind the obstruction is initially the larger of the two piles, but later they coalesce into one mound, which is the beginning of dune formation (Lancaster 1995). The shape that dunes take depends on wind velocity and sometimes on the amount of sand available. Dunes may form in a number of ways:

2.4.1.1.1 Barchan dunes These usually are formed on the margins of deserts where the wind direction is generally more uniform and the amount of sand is moderate (Mesbahzadeh and Ahmadi 2014). The tips of the crescent (Fig. 2.12) point downwind and are lower than its centre, where air flow is impeded most and sand accumulates in larger quantities. Some of these dunes can be rather high. The complex transverse megadunes, which resemble the barchan dunes in terms of wind direction and amount of sand, range in height between 180 and 350 m and may reach as much as 400 m in the Badain Jaran Desert (part of the Alashan Desert, in turn part of the Gobi Desert) (Dong et al. 2004).

2.4.1.1.2 Seifs or longitudinal dunes where sand is more plentiful, a steady wind creates transverse dunes shaped similar to long waves with crests perpendicular to the wind and with gentle windward slopes (lee slopes are often called the slip face) (Fig. 2.13). Bristow et al. (2005) consider this to be the most abundant type of desert dune. Bristow et al. (2007) have shown that longitudinal dunes (also known as linear dunes) are not fixed in space and may move considerably (about 300 m or more) under certain wind conditions. Bristow et al. (2007) have also shown that longitudinal dunes in the Namib Desert may undergo several phases of construction. One

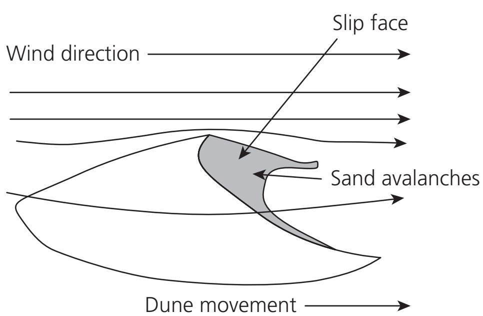

Fig. 2.12 Schematic diagram of a barchan dune.
Source: This U. S. National Park Service file is under the Creative Commons License.

Fig. 2.13 Linear dunes (viewed from above) in the Great Sand Sea in southwestern Egypt, part of the Sahara Desert. Wind from the north moves the sands into linear dunes that are aligned parallel with the winds.

Source: Photo from N.A.S.A.

dune had a hiatus of about 2,000 years and took a total of about 5,700 years to construct to its current height. Seif and longitudinal dunes may exceed 40 m in height and may extend for hundreds of kilometres, sometimes as much as 250–400 km (e.g. in the Sahara, Namib Desert, Thar Desert in India, and the western part of the Great Australian Desert). Where wind directions are less well defined, both barchan and seif systems may merge into areas of complete sand cover (Flegg 1993).

2.4.1.1.3 Star dunes If the sand is confined to a basin, and the wind periodically radically changes its direction, the resulting dunes will become complex in shape and may be called star dunes (Fig. 2.14).

2.4.1.1.4 Loess The German word 'löß' was created by Von Leonhard (1824) to describe the silty deposits along the Upper Rhine valley. This was then called 'loess' in English by Lyell (1832). Loess is an important form of wind-blown silt deposit, which even on the least windy days can form a fog of dust (Pye 1987; Goudie 2009). Loess consists mostly of quartz, feldspar, mica, clay minerals, and carbonate grains in varying proportions (Pye and Tsoar 2009). Pecsi (1990) notes that loess must refer to something more than aeolian dust and must contain reference to the specific mode of genesis of the material and landforms, linking it explicitly to arid and semi-arid landforms.

Many researchers considered loess to be the product of glacial erosion ('grinding' (Hardcastle 1889; Smalley 1966)). This resulted in researchers in Australia not considering their fine, aeolian silt deposits to be loess because of the absence of glaciation in Late Pleistocene Australia (Haberlah 2007). Butler (1956) also noted that Australian loess had higher clay content than loess from other parts of the world and called the Australian form 'parna'. Later, Pye (1995) recognized that clay content was not

Fig. 2.14 Star dunes are the dominant dune type in the southern edge of the Grand Erg Oriental in northeastern Algeria. These pyramid-shaped star dunes form because the winds blow from multiple directions.

Source: Photo under Creative Commons licence.

crucial to the formation of loess and could be formed by variable calcium carbonate and clay contents. Furthermore, new research reveals that there are other weathering forces and sediment transport processes that can create loess (Haberlah 2007).

Strong winds can carry these dust particles many thousands of kilometres. White dust in the summer and red dust in the winter can spread from the Sahara and the Arabian deserts over the Mediterranean Sea, even reaching as far as Sweden (Page 1984). The highest dust storm frequencies occur in the arid and semi-arid regions of the world, with a mean frequency of about 81 days when visibility at eye level is less than 1,000 m has been recorded (e.g. in the Seistan Basin of Iran; Middleton 1986). Pye (1987) has noted that the frequency of dust storms shows a weak negative relationship with mean annual precipitation, with areas receiving 100–200 mm rainfall having markedly higher dust storm frequencies. Goudie (2009) suggested that this may occur because infrequent stream run-off limits dust supply or because strong winds associated with storm fronts and cyclonic disturbances are rare in these areas. In contrast, the higher dust storm frequencies could be related to greater fluvial activity, greater dust supply, and more frequent strong winds. Pye and Tsoar (2009) believe that it is likely that recent cultivation is an important source of dust on desert-margin soils.

The Loess Plateau in China (also known as the Huangtu Plateau) contains some of the most impressive loess deposits recorded anywhere. It covers about 640,000 km^2 around the Huang He (Yellow River). Pye (1995) considers the remarkably thick loess of the Loess Plateau in China to result from an unusual combination of conditions which has persisted for much of the past 2–3 million years, specifically due to the rapid uplift of the Tibetan Plateau and surrounding mountain ranges, high rates of sediment production and supply to adjacent basins, a strong northwesterly and westerly wind regime, and the existence of effective dust traps downwind of the source regions. Guo et al. (2002) indicate that large source areas of aeolian dust (and energetic winter monsoon winds to transport the material) must have existed in the interior of Asia by the early Miocene epoch, 22 million years BP, which is at least 14 million years earlier than previously thought. Liu et al. (1981) recorded that dust that had been transported from the deserts of northwestern China to Beijing (more than 3,000 km) contained greater than 90% of its particles that were less than 30 μm in size. The initial desertification in the Asian interior is thought to be one of the most prominent climatic changes in the Northern Hemisphere during the Cenozoic era (65 million years ago). However, the dating of this transition is uncertain, partly because desert sediments are usually scattered, discontinuous, and difficult to date.

2.4.1.2 Saline soils

Soils that form in desert climates are predominantly mineral soils with low organic matter content. However, the repeated accumulation of water in certain soils causes salts to precipitate out. When the water table rises to within about 2 m of the ground level, water may begin to rise to the surface by capillary action. When a rising water table intersects with salts that were previously held below the root zone, the salt will dissolve and be carried up to the surface, concentrating in the upper layers of the soil as water is evaporated. Most playa lakes will consequently be highly saline (Yu et al. 2012).

Salinity is typically measured as electrical conductivity (EC), in deciSiemens m^{-1}. Seawater is typically 50–55 dS m^{-1} (Brinkman 1980; Table 2.1). When soil salinity exceeds about 2 dS m^{-1}, agricultural crops will generally fail. Salinity disrupts the ion exchange mechanism between soil moisture and plant cells. As a result, plant cells dry out, plants wilt, and, therefore, salinity steadily rises. Harmful quantities of nutrients or trace minerals (such as boron, copper, manganese, and zinc) can also

Table 2.1 From the FAO/UNESCO soil map of the world, the following percentages of salinized areas can be derived

Continent	% Salinized area
Africa	69.5
Middle East	53.1
Asia	19.5
South America	59.4
Australia	84.7
North America	16.0
Europe	20.7

Source: Brinkman (1980).

damage or kill a plant. Salinity changes the electrochemical balance of soil particles. It also destroys physical soil properties, reduces its draining capacity, and increases evaporation and soil erosion.

2.4.1.3 Stone

Stone substrates usually have relatively level gravel surfaces. This is known as desert pavement (also known as *reg*—Fig. 2.15), which is a dense cover of rocks too large to be carried away by wind or water. Silt, sand, and smaller pebbles have been removed by a gradual erosive process called deflation (Matmon et al. 2009). Once thought to originate from either deflation or expansion and contraction of wet desert soils, desert pavement is now known to form *in situ* from the aeolian accumulation of dust beneath a surface layer of gravel (Dickerson 2012). Matmon et al. (2009) have found that these surfaces may experience erosion rates that are slower than those documented elsewhere on Earth and can retain their original geometry for more than 2 million years. Desert pavement affects the type and distribution of desert plants on arid land surfaces (Martinez-Berdeja et al. 2013), as well as inhibits the activities of small burrowing animals (Bouskila 1983; Wilms et al. 2009). After a long time, the remaining stones settle into a coarse mosaic, resembling a street paved with cobblestones (hence the name *desert pavement*), which presents a shield against further erosion.

Desert pavement is frequently coated with desert patina (also known as *desert varnish*), which is a black or brown coating on the outer surface of the rocks (Fig. 2.16). This gives a similar veneer to the rocks of various different compositions, created by oxides of iron and manganese and deposited by wind and water from rain and dew. This process takes thousands of years. In the Sinai Desert, thousands of square kilometres are covered with reg.

Fig. 2.15 Desert varnish on reg or gibber from central Australian desert.
Source: Photo by Mark Marathon under Creative Commons licence.

Fig. 2.16 Desert patina with giraffe engraved on the thin outer surface of iron/manganese at Twyfelfontein in the Namib Desert, Namibia. Note the seal, indicating that the people were also aware of or traded with people who caught seals.

Source: Photo courtesy of Megan Griffiths.

2.4.1.4 Rock

Rock desert landscapes normally have bare rock surfaces, with a huge pavement kept clear of sand and gravel by the wind.

2.4.1.4.1 Plateaux Rocky plateau landscapes are often deeply dissected by ephemeral rivers (wadis). In some cases, notable repetitions of anticlines and synclines occur. This occurs in a desert landform known as *mountain-and-basin* desert (Ezcurra 2006). An anticline is a trough-like upfold of the earth while a syncline is a trough-like downfold (Strahler 1976). In a few cases, anticlines may erode through the soft rock at the top, creating a wadi along its length. Such an anticline is known as an erosional cirque (Ben-David and Mazor 1988; Plakht 1996) or *makhtesh* (Hebrew) (Fig. 2.17). They are only known from the western edge of the Arabian Desert in Israel, Jordan, and Syria (Plakht 1996).

2.4.1.4.2 Mountain Mountain desert landscapes are bare arrays of rocky peaks, such as in the Sinai portion of the Arabian Desert and the granitic areas of the Namib Desert (Fig. 2.18). These mountainous deserts constitute a second landform (see *mountain-and-basin* desert in the previous section) called a *shield* desert, which has very old igneous rocks. This includes the Sinai Desert, as well as the Australian and southern African deserts and the Sahara. Unlike the mountain-and-basin deserts, wind is a more effective force than water in shield deserts. Note that the Australian deserts are, topographically speaking, extremely flat (Stafford Smith and Morton 1990); therefore, mountains are found only in a few places. Nonetheless, the Australian mountains that occur consist of old igneous rocks. As the rates for slopes and valleys exceed crest rates, Quigley et al. (2007) and Fujioka and Campbell (2011) infer that relief is increasing in Australian deserts.

Fig. 2.17 Satellite photograph of Makhtesh Katan, a Negev Desert erosion cirque.
Source: Photo from Wikipedia Creative Commons.

Fig. 2.18 Granitic hills of the Namib, near Spitzkoppe.
Source: Photograph courtesy of Megan Griffiths.

2.5 Fire

Generally, fire is not considered as an important factor in desert ecosystems because fuel loads (created primarily by grasses) are generally too low (Meyer et al. 2005).

However, McPherson (1995) considered three conditions for fires to spread, namely, an ignition source, sufficient fine fuel, and the fuel must be sufficiently dry to burn. All of these conditions occur in the North American desert grasslands (Allen et al. 2011; McDonald and McPherson 2013; Ladwig et al. 2014). They occur in some other deserts too, particularly in Australia (Orians and Milewski 2007; Bowman et al. 2008). In North American desert grasslands, there is sufficient fine fuel from the grasses and the fuel is dry enough to burn. This is exacerbated in some circumstances by the presence of fire-tolerant invasive grasses (Brooks and Chambers 2011), such as buffelgrass (*Pennisetum ciliare*; McDonald and McPherson 2013). Lightning storms prior to the onset of monsoon rains in June or July provide opportunities for fires to ignite in desert grasslands of North America (McPherson 1995). Humphrey (1958) reviewed historical fire accounts dating back to 1528 in the North American desert grasslands and considered fires critical to the maintenance of these grasslands by preventing them from succeeding towards shrubs and trees. Ladwig et al. (2014) found that Sonoran Desert fires were not dependent on season of burn (autumn, spring, or summer) but were more likely to burn after droughts.

In Australia, spinifex grasslands (mostly *Triodia* species) and many woody desert plants are renowned for their ability to burn (Stafford Smith and Morton 1990; Orians and Milewski 2007). Spinifex plants have high resin contents and they have low levels of nutrients (which means that consumption rates by herbivores are low) and decomposition rates of ligneous litter are also low. Thus, litter and standing biomass accumulate rapidly in some areas (Stafford Smith and Morton 1990). Fires may range in intensity from ground fires that consume litter and small plants to stand-destroying fires that kill all plants such that they are unable to resprout from underground storage organs (Orians and Milewski 2007). Bowman et al. (2008) examined repeat aerial photography over 52 years (1950–2002) of the boundaries between *Acacia aneura* woodlands and adjacent *Triodia* grasslands in arid Australia. There was some variability in the size of the *Acacia aneura* patches, but the differences were small (over the entire period, there was only a change of 3.1%, with a maximum change of 13.1% (decrease) occurring between 1950 and 1983). Fire effects on boundaries were mediated by the size of *Acacia aneura* patches, with small patches most likely to contract. Bowman et al. (2008) concluded that a series of reinforcing fire, soil, and vegetation feedbacks maintain the mosaic of shrubland patches. However, these feedbacks might eventually be overwhelmed by large and sustained changes to fire regimes, leading to the landscape-wide dominance of *Triodia* grasslands. This contrasts with the global observations of invasion of arid grasslands by shrublands.

2.6 Wind erosion

Wind erosion is one of the most powerful forces in deserts (Goudie 2008). This is particularly true in sandy deserts but it is also a major factor in rocky deserts, particularly where wind has sufficient distance to build up speed. It is responsible for blowing sand over large distances and erosion of rocks. Even the granite rocks of the Spitzkoppe in Namibia are susceptible to this (Matmon et al. 2013; Fig. 2.18). Li et al. (2008) found that there are large potential changes in the heterogeneity of soil nutrients such as organic carbon, total nitrogen, nitrogen availability, and sulphates. However, Li et al. (2008) also found that cations such as Ca^{2+} and Mg^{2+} were not significantly redistributed. Other ions such as K^+, Na^+, and Cl^- showed no obvious pattern of change in their study at the Jornada Experimental Range in the Chihuahuan Desert. In encroached areas, the changes in the distribution of nutrients were focused on large fertile islands of fertility around *Prosopis* shrubs. There are also many plant species affected by wind erosion, ranging from cyanobacteria (Belnap et al. 2007) to flowering plants (Bang et al. 2010). Seed dispersal may be greater in windy desert areas, such as playas (Fort and Richards 1998).

3 Morphological and Physiological Adaptations of Desert Plants to the Abiotic Environment

Some of the most interesting adaptations of plants to their environments are shown by desert plants. One need to only think of the cacti of North and Central America (Gorelick 2009), spinifex (*Triodia* spp.) in Australia (Nano and Clarke 2008), *Welwitschia mirabilis* of the Namib (Henschel and Seely 2000), and the Mesembryanthema (Aizoaceae) of the Karoo in South Africa (Klak et al. 2004) to realize that deserts contain a uniquely adapted flora. Geophytes and other plants with special storage organs may be considered to be pre-adapted to desert conditions (Shmida and Dafni 1990; Viruel et al. 2012), while trees and shrubs with deep root systems are able to exploit deep aquifers in an otherwise dry environment (Ward et al. 2013). Many annual plants do not have clear morphological or physiological adaptations to the desert environment but thrive there by germinating immediately after the infrequent rains and completing their life cycles before the onset of the summer heat (Guo et al. 2002; Allington et al. 2013). This chapter will also examine the various ways in which mesic plants have been able to exploit resource variability to survive in extreme desert environments.

3.1 Classifications of desert plants

There are several ways to approach the study of desert plants and their relationships with their abiotic environments (cf. Shantz 1927; Raunkiaer 1934; Evenari 1985; Danin and Orshan 1990; Smith et al. 1997). For example, Shantz (1927) classified desert plant strategies in terms of their abilities to tolerate or avoid drought:

1. *Drought escaping*—plants that grow only when water is available. These are usually annual plants that are ephemeral and restrict their growth to those periods, usually in the spring, when there is sufficient water for plant growth and reproduction.
2. *Drought evading*—these plants avoid periods of limited soil moisture by using morphological features such as deep roots (e.g. in riparian trees from southern Africa such as camelthorn, *Acacia erioloba*, and shepherd's tree, *Boscia albitrunca*,

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which have roots as deep as 68 m (Jennings 1974)), stem succulence (e.g. cacti in the Americas and euphorbs in Africa), and/or physiological features such as stomatal control of water loss and crassulacean acid metabolism (CAM) photosynthesis. Drought avoidance is characterized by stomata that close at higher water potentials and larger leaves with less vertical orientation and less ability for the accumulation of solutes and/or maintenance of high tissue elasticity (Smith et al. 1997). Inward contraction of elastic walls can cause a loss of volume, allowing for the maintenance of turgor pressure (Smith et al. 1997). Monson and Smith (1982) showed that maintenance or seasonal adjustment of low osmotic potentials was negatively correlated with drought avoidance (Fig. 3.1).

3. *Drought enduring*—these plants possess rapid gas exchange (with less stomatal control of water loss) and shed their leaves when droughts occur. This includes most desert shrubs, such as *Hammada scoparia* (Chenopodiaceae) in the Middle East.
4. *Drought resisting*—these plants have moderate rates of gas exchange when water is plentiful but are able to maintain some reduced level of gas exchange during periods of water stress. These plants are characterized by having stomata that close at low plant water potentials, small leaves with a tendency for vertical orientation,

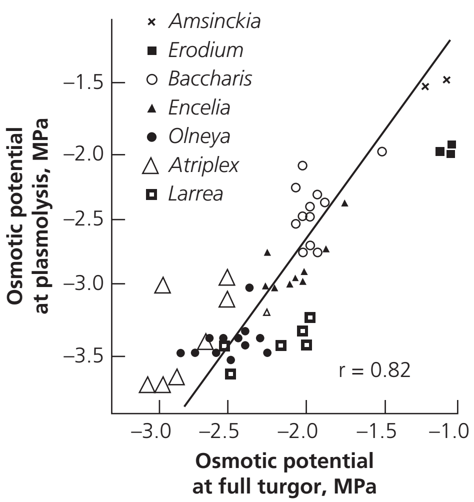

Fig. 3.1 Monson and Smith (1982) found a strong positive correlation between water potential at full turgor and water potential at plasmolysis (also called the turgor loss point), which indicated that maintenance of low osmotic potentials was negatively correlated with drought avoidance. The species involved were *Amsinckia intermedia* and *Erodium cicutarium* (both annual herbs), *Olneya tesota* (evergreen tree), *Larrea tridentata* (evergreen shrub), *Baccharis sarothroides* (evergreen tree or shrub), *Atriplex polycarpa* (evergreen halophyte shrub), and *Encelia farinosa* (drought-deciduous shrub). Note that the axes are reversed.

Source: From Monson and Smith (1982). With kind permission of Springer Science and Business Media.

low hydraulic conductance of the xylem, and high capacity to accumulate solutes and/or maintain high tissue elasticity to ensure turgor maintenance (Smith et al. 1997). Only a few plants fall into this category, including the creosote bush *Larrea tridentata* and some plants in Middle Eastern deserts, such as *Zygophyllum dumosum* and *Anabasis articulata* (Plate 9). Note that *drought tolerance* is a synonym for *drought resisting*. In addition, the terms *drought stress, water stress*, and *water deficit* are often used interchangeably.

One limitation to this categorization is that it does not accommodate the mistletoes (Loranthaceae and Viscaceae) (Fig. 3.2). These hemiparasitic plants are capable of photosynthesizing but do so at the expense of their hosts, from which they gain water and nutrients (Bowie and Ward 2004; Okubamichael et al. 2011). Through passive water uptake, mistletoes open their stomata and transpire profligate amounts of water from the xylem to access nutrients such as nitrogen. Some mistletoes (e.g. *Viscum rotundifolium*, which grows on a number of plants, especially *Ziziphus mucronata* and *Ehretia rigida*) also take up water from the phloem using active water uptake, which does not require large amounts of water (Okubamichael et al. 2011).

Raunkiaer (1934) developed an alternative classification system based on the strategy a plant uses to protect its perennating buds (growing points), noting that plants will maximize the survival of these buds during dry or cold seasons (not all of Raunkiaer's (1934) types are listed here because some are not pertinent to plants growing under xeric conditions):

1. *Therophyte*—annuals (Plate 10).
2. *Phanerophyte*—the surviving buds or shoot apices are borne on shoots which project into the air.

Fig. 3.2 Desert mistletoe, *Phoradendron californicum*, on foothill Palo Verde, *Parkinsonia microphylla*.

Source: Photo by Linda and Dick Buscher.

3. *Chamaephyte*—a perennial plant that sets its dormant vegetative buds just at or above the surface of the ground and that dies back periodically. Usually, the difference between the phanerophytes and chamaephytes is somewhat arbitrary but differentiates trees (phanerophytes) and shrubs (chamaephytes—Plate 11).
4. *Cryptophyte*—plants whose buds develop underground or underwater. In the terrestrial case, they can be divided into:
   a. *Geophyte*—a perennial plant that propagates by underground bulbs, tubers, or corms (Plate 12).
   b. *Halophyte*—plants living under or near saline conditions.
5. *Hemicryptophyte*—the surviving buds or shoot apices are situated in the soil surface and die back during unfavourable conditions.
6. *Vascular hemiparasite*—parasitic plants that photosynthesize, e.g. mistletoes such as *Plicosepalus acaciae* (Loranthaceae, Middle East) or root parasites such as *Santalum acuminatum* (Santalaceae, Australia).
7. *Vascular parasite*—plant that is entirely dependent on other plants, including root parasites such as *Orobanche* (Orobanchaceae) in the Negev Desert (Fig. 3.3) and stem parasites such as *Cuscuta* (Cuscutaceae or Scrophulariaceae, depending on the classification).

Raunkiaer's (1934) classification system is probably most appropriate for buds escaping freezing rather than dry conditions (Danin and Orshan 1990; Smith et al. 1997). The limitation of this classification system in desert scenarios is that plant water and carbon relations during favourable seasons may be more important in determining the success of plants than the location of buds (Schulze 1982). For example, phreatophytes are deep-rooted plants (usually trees) that use the water table or some other permanent water supply (Ward et al. 2013). Nonetheless,

Fig. 3.3 A root parasite, *Cistanche tubulosa*, growing on *Purple Island* in Qatar.
Source: Photo by Alexey Sergeev under Creative Commons licence.

Raunkiaer's (1934) system is widely used, although one needs to be aware of the fact that it is somewhat limited in its generality. Overall, a structure–function classification is the most useful way to categorize desert plants (see also Danin and Orshan 1990; Smith et al. 1997).

3.2 Types of photosynthesis

Before embarking on the analysis of relationships between plants and their desert environments (reviewed in Table 3.1), it is important to consider some basics of photosynthesis that allow a plant to convert carbon dioxide into sugars (carbohydrates). There are three major types of photosynthesis:

Table 3.1 Adaptive characteristics of the major structural/functional groups of plants in the deserts of North America

Adaptation	Structural/functional group					
	Annuals	Perennial grasses	Deep-rooted trees	CAM succulents	Deciduous shrubs	Evergreen shrubs
Small leaves	Typically not	Yes, but dense	Variable, usually small	No	Variable, many broad	Yes
Waxy cuticle, sunken stomata	No	No	No	Yes	Variable	Yes
Shallow roots	Yes	Variable, usually yes	No	Yes	Variable, usually yes	Variable
High root:shoot ratio	No	Variable	Variable	Mass: no Area: yes	Variable	Variable, often high
High water stress tolerance	No	Variable, some yes	No	Plant: yes Tissues: no	Variable, usually yes	Yes, very high
High heat tolerance	No	C_3: no C_4: yes	No	Yes, very high	No	Yes
Low photosynthetic and growth rates	No	No	No	Yes	No	Yes
High water-use efficiency	No	No	No	Yes	Variable	Yes
High nutrient-use efficiency	No	Variable	No	Yes	Variable	Yes
Opportunistic phenology	Yes	No	No	No	Variable	No

Source: After Smith et al. (1997).

1. *C_3 photosynthesis*—it is most common for plants to use the C_3 metabolic pathway, which means that CO_2 is attached to the 5-carbon sugar RuBP (ribulose bisphosphate) with the assistance of the enzyme RuBP carboxylase-oxygenase (also known as Rubisco) and will then be converted into sugar. There are two phosphoglycerate (PGA) sugar molecules produced by this form of photosynthesis. There are C_3 molecules, hence the name of this photosynthetic pathway. C_3 photosynthesis is a diurnal process. The ratio of CO_2 to O_2 is very low, resulting in a considerable amount of photorespiration, which results in a lower level of net photosynthetic efficiency than in C_4 plants (about one-third lower efficiency). C_3 photosynthesis is considered the most simple and least derived photosynthetic pathway (Ehleringer and Monson 1993). Despite the fact that this form of photosynthesis is energetically expensive, it occurs in many desert plants, especially dicotyledonous plants.
2. *C_4 photosynthesis*—the C_4 pathway is used by angiosperms, often in arid environments (i.e. with high light levels and temperatures) that have a lot of water available to them in the summer (Edwards and Smith 2010). Edwards and Smith (2010) found that 18 of 20 inferred C_4 origins were correlated with marked reductions in precipitation. These authors concluded that C_4 evolution in grasses was consistent with a shift out of tropical forest environments into tropical woodlands and/or savannas. C_4 photosynthesis also occurs diurnally as does C_3 photosynthesis. Here, CO_2 is converted into oxaloacetate (a C_4 sugar) by phosphoenolpyruvate (PEP) carboxylase and then into a sugar (either malate or aspartate) by ribulose-1,5-bisphosphate (RuBP) carboxylase (Rubisco) inside the bundle sheath cells. The PEP carboxylase is more efficient than Rubisco because it matches its substrate better, has greater velocity than Rubisco, and effectively acts as a CO_2 pump. C_4 plants still use the C_3 method in their internal cells (typically the bundle sheath) but their external mesophyll cells use the C_4 method. There is a distinct spatial segregation of the bundle sheath cells where C_3 photosynthesis occurs and the exterior mesophyll cells where C_4 photosynthesis occurs. This is created by a structure known as Kranz anatomy (Ehleringer and Monson 1993). The Rubisco reactions in C_4 plants take place under higher CO_2/O_2 levels and photorespiration is effectively eliminated. Griffiths et al. (2013) found that the origin of bundle sheaths was associated with maintaining leaf hydraulic conductance and cavitation repair under increased evaporative demand and more seasonal precipitation. This occurred under declining CO_2 concentrations during the Palaeogene and Neogene.
3. *CAM (Crassulacean acid metabolism)*—this photosynthetic pathway is employed by many succulent plants such as aloes, cacti (Cactaceae), agaves (Agavaceae or Agavoideae), euphorbias (Euphorbiaceae), ice plants (Mesembryanthema, Aizoaceae—Plate 13), and crassulas (Crassulaceae; from which the name of the photosynthetic pathway is derived). The CAM pathway is used in deserts that have high light levels, high temperatures, and low levels of moisture in the summer. Thus, one major difference between C_4 photosynthesis and CAM is that C_4

photosynthesis takes place when water is readily available while CAM is restricted to low water conditions. CAM photosynthesis takes place in two stages. The first stage takes place nocturnally when the stomata of the plant are opened. CO_2 enters the leaf through the open stomata and is fixed and stored as an acid (usually malic acid). The second stage of the CAM process takes place diurnally while the stomata are closed. The CO_2 is released from the malic acid and is then used to make sugar with the aid of RuBP carboxylase. While C_4 plants use a different *spatial* strategy for C_3 photosynthesis (Kranz anatomy), CAM plants have a different *temporal* strategy for C_3 photosynthesis (night vs day).

CAM plants may also employ C_3 photosynthesis when conditions improve but never use C_4 photosynthesis. A point worth noting is that all adult CAM plants start off life as C_3 plants (Raven and Spicer 1996). An interesting example of a switch between CAM (i.e. nocturnal photosynthesis) and diurnal photosynthesis occurs in *Agave deserti* (Agavaceae or Agavoideae), which changes photosynthetic pathway when given supplemental water (Hartsock and Nobel 1976) (Fig. 3.4).

Compared with other pathways, C_4 photosynthesis requires two extra molecules of adenosine triphosphate (ATP) to reduce a CO_2 molecule, which should make C_3 photosynthesis more light-use efficient. However, this only occurs at leaf temperatures below about 25–30°C (Ehleringer and Monson 1993). Above this temperature range, there is a negative effect of photorespiration on C_3 photosynthesis. Because there is no temperature constraint on C_4 and CAM photosynthesis, these two photosynthetic pathways have a greater light-use efficiency at high temperatures. C_4 photosynthesis is also more water-use efficient because the greater CO_2 pump activity of PEP carboxylase makes it mostly independent of CO_2 inside the leaf. Furthermore, changes in the degree of stomatal opening exert little influence on photosynthetic rates in C_4 plants over a broad range of stomatal openings. However, rates of transpirational water loss are directly proportional to the degree of stomatal opening in C_3 and C_4 plants. Therefore, water-use efficiency (the ratio of

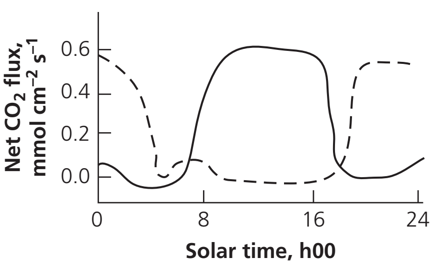

Fig. 3.4 Conversion in photosynthetic pattern (measured as CO_2 flux) from CAM (dashed line) to diurnal photosynthesis (solid line) in *Agave deserti* after watering. Soil water potentials were raised from −9 to −0.01 MPa. Note the switch from nocturnal CO_2 flux under CAM conditions to diurnal CO_2 flux under watered conditions.

Source: From Hartsock and Nobel (1979). With kind permission of Nature Publishing Group.

photosynthesis:transpirational water loss) is higher in C_4 plants than in C_3 plants. CAM plants have an even higher water-use efficiency than C_4 plants because their stomata are only opened at night, when transpirational water loss is low. Thus, at equivalent rates of water loss, a C_4 or CAM leaf is expected to photosynthesize more than an adjacent C_3 leaf operating under the same set of environmental conditions (Ehleringer and Monson 1993). One would expect that C_4 and CAM plants should occur under more arid conditions than C_3 plants. In the North American deserts, C_3 plants typically occur in the winter rainfall Mojave Desert, C_3 and C_4 plants in the summer and winter rainfall Sonoran Desert, and mostly C_4 plants in the summer rainfall Chihuahuan Desert (Ludwig et al. 1988; Smith et al. 1997; Huxman and Monson 2003). In the Chihuahuan Desert, Eickmeier (1978) found that, of 88 species, the dominant plants changed from CAM to C_4 to C_3 as aridity declined, although CAM plants tend to be somewhat bimodally distributed (Eickmeier 1978). CAM plants occupy the most arid sites along the Californian and Chilean coasts (Mooney et al. 1974). In semi-arid southwestern Madagascar, succulent CAM plants of the families Euphorbiaceae and Didiereaceae are predominant (Winter 1979). Along a gradient of desert to Mediterranean climate in the northern Sahara Desert, δ^{13} C isotopes have been used to identify C_3 and C_4 plants. Typically, C_4 plants have higher values (−9 to −16‰) than C_3 plants (−25 to −32‰) (Winter et al. 1978; Ehleringer 1993). Winter et al. (1978) found that C_3 species predominate in the Mediterranean region and the C_4 species in the desert.

Contrary to the expectation that C_4 grasses predominate in hot, dry climates, Hattersley (1983) examined the distribution of C_3 and C_4 grasses relative to climate in Australia and concluded that C_4 species are most abundant where summers are hot and wet and decline with decreasing temperature and/or decreasing summer rainfall, whereas C_3 species are most numerous where the spring is cool and wet and decline with increasing temperature and/or decreasing spring rainfall. Similarly, in the cold winter Great Basin Desert, both C_3 and C_4 plants are common strategies (Caldwell et al. 1977). In the very hot and arid Death Valley of California, both C_3 and C_4 plants grow in close proximity (Mooney et al. 1974). It appears that C_3 and C_4 plants can coexist in deserts such as the Namib, Great Basin, and Negev (Vogel and Seely 1977).

Summer temperatures through most of Namibia are remarkably uniform (around 30–40°C), except for the cooler temperatures (about 20°C) of the narrow Atlantic Ocean coastal region. While ambient temperature is relatively high, rainfall exhibits a gradient from about 10 mm to more than 600 mm per annum in a northeasterly direction. C_4 grasses are dominant throughout Namibia. In the central Namib Desert, non-grass species are mostly C_3 (Vogel and Seely 1977). C_3 grass species have a limited distribution, making up about 18% of the grass species in the dry southwest of the Namib Desert with winter rainfall and about 15% of species in the mesic northeast. Clearly, C_3 grasses cannot be restricted by rainfall, being present at either end of the rainfall gradient. However, in the low rainfall areas of the southwest Namib, they tend to favour moist microhabitats (Ellis et al. 1980).

Nonetheless, it appears that plants with different types of C_4 photosynthesis differ in their responses to rainfall in Namibia. All C_4 grasses have Kranz anatomy and initially fix CO_2 in the mesophyll cells, which results in the formation of oxaloacetate and is converted into either malate and/or aspartate. Depending on the relative quantities of malate and aspartate formed, two distinct groups of C_4 plants are recognized (Gutierrez et al. 1974; Edwards et al. 2001):

1. Aspartate formers with an inner bundle (mestome) between the metaxylem elements and the Kranz sheath. There are two subtypes of aspartate former: those using PEP-carboxykinase (PEP-ck) and those using nicotinamide adenine dinucleotide (NAD)-malic enzyme (NAD-me). PEP-ck species have centrifugally located chloroplasts that lie against the outer wall of the Kranz sheath cells while the NAD-me species have centripetally located chloroplasts.
2. Malate formers with a single chlorenchymatous or Kranz sheath and centrifugal chloroplasts formed around the vascular bundles. The malate formers lack well-developed grana in the chloroplasts and have a low mitochondrial frequency. Also, malate formers do not show a post-illumination CO_2 'burst' as the aspartate formers do.

Ellis et al. (1980) found that malate formers increased in abundance relative to rainfall (contrary to the expectation if they were true arid-zone plants), NAD-me aspartate species decreased in abundance with increasing rainfall, while PEP-ck aspartate-forming species were intermediate in their distributions. Thus, the type of C_4 distribution may be affected by climate, with NAD-me species more common in truly xeric areas.

There are also a number of interesting phylogenetic and biogeographic issues involved in explaining the patterns of photosynthesis observed today (Ehleringer and Monson 1993). For example, C_4 photosynthesis has evolved at least three times in the grasses (Poaceae) (Brown and Smith 1972) and at least twice in the widespread genus *Atriplex* (Chenopodiaceae). Brown and Smith (1972) have examined the presence of C_4 photosynthesis in the grasses and have shown that it is consistent with Wegener's (1966) notion of continental drift. For example, they showed that the tribes Eragrostoideae and Aristideae have Kranz anatomy (i.e. they are C_4 species) and are found in all the major deserts of the world, which can only be explained by the presence of a single continent of Pangaea. Johnson (1975) analysed about 1,000 desert species in California and found that about 85% were C_3, 11% were C_4, and 4% were CAM. However, Johnson (1975) found that more than half the C_4 species were grasses (Poaceae). In the Crassulaceae, the group for which CAM is named, North American species exhibit only CAM recycling, which means that there is C_3 uptake of CO_2 with capacity to recycle respired CO_2 at night. However, full CAM ability has evolved at least twice in trans-Mexican species (Ehleringer and Monson 1993). Another interesting point is that C_4 dicotyledons do not follow the climate relationships that have been reported for C_3 monocotyledons. Stowe and Teeri (1978) found that the representation of dicot species in local floras of North America was more highly correlated with indices of aridity than indices solely describing temperature.

However, even C_3 species in those families that contained C_4 dicots exhibited significant correlations with aridity, suggesting a phylogenetic component independent of photosynthetic pathway. Assuming that C_3 photosynthesis was ancestral in these families, the results suggest a pattern of C_4 evolution in those North American dicot taxa predisposed to growth in arid habitats. Nonetheless, Evenari (1985), and Ehleringer and Monson (1993) after him, considers it an unresolved issue and assumes that there must be a trade-off between photosynthetic ability and competition under conditions of high temperature (with C_3 plants being more effective and competitively dominant at lower temperatures and C_4 plants being dominant at higher temperatures because of their greater water-use efficiency). Should researchers have studied the different forms of C_4 photosynthesis, as Ellis et al. (1980) did (see earlier discussion in this section), they may have been able to understand whether it is the subtype rather than merely the type (i.e. C_3 vs C_4) that differs.

3.3 Biological soil crusts

In arid and semi-arid parts of the world, autotrophic organisms occur in the open spaces between higher plants. These organisms are called biological soil crusts (Fig. 3.5; Plate 14) or, alternatively, cryptogamic, cryptobiotic, microbiotic, or microphytic communities (Belnap et al. 2013; Büdel et al. 2013). In general, the greater the vegetative cover of higher plants, the lower the cover by biological soil crusts. Biological soil crusts differ from mechanical and chemical crusts. Mechanical and chemical crusts are formed by clays or salts in the soils. Biological crusts, on the other hand, are formed from a combination of cyanobacteria, algae, lichens, mosses, bacteria, and fungi. Mechanical and chemical crusts tend to cause run-off of surface flow, increasing loss of precipitation from an ecosystem (Savory 1988), while biological crusts increase infiltration and thus have positive local effects. They may also increase nitrogen fixation (5–88% of nitrogen fixed by a cyanobacterium is released to neighbouring vascular plants) (Belnap and Harper 1995), reduce wind and water erosion, and contribute to local soil organic matter (Eldridge and Greene 1994).

Biological crusts may constitute as much as 70% of the cover of biological organisms in a particular community. Structurally, they form a low surface of 1–10 cm above ground. Below ground, they bind the soil or sand together by means of cyanobacterial filaments, fungal hyphae, and moss and lichen rhizines (a root-like filament growing from moss and lichens). These organisms are capable of withstanding desiccation and suspending respiration with no apparent negative effects (Belnap et al. 2013), unlike vascular plants that either regrow or die. These organisms are considered poikilohydric and often equilibrate their activities with that of atmospheric humidity or soil moisture content (Belnap et al. 2013). They can appear dark or black (especially cyanobacteria) until they photosynthesize, when they change colour (to green) within a few minutes. These organisms require relatively high levels of hydration to photosynthesize. Belnap et al. (2013) found that run-off and erosion were greatest for the lowest level of development of the biological soil crust.

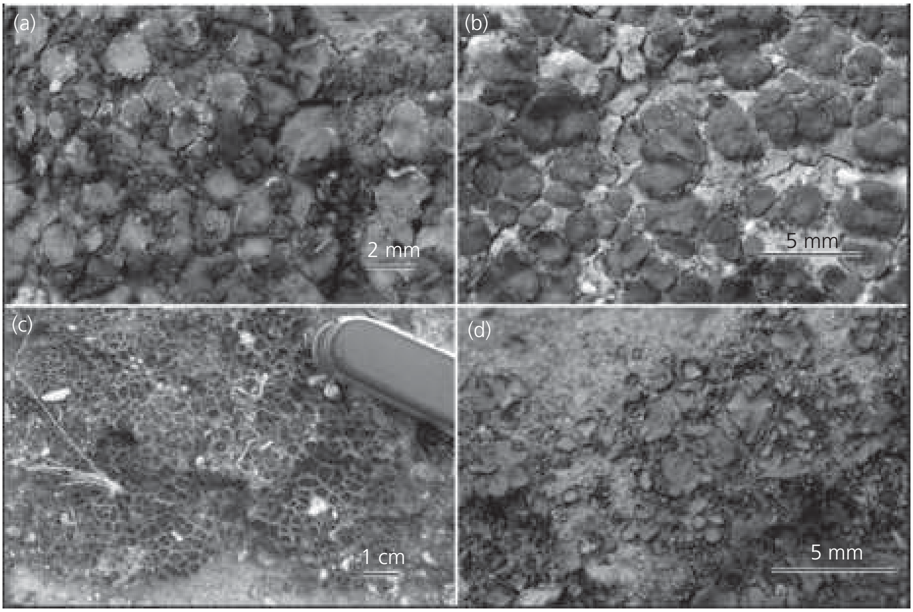

Fig. 3.5 Biological soil crust types with different dominating lichen species from Baja California, Sonoran Desert, Mexico: (a) chlorolichen *Psora decipiens*; (b) chlorolichen *Placidium squamulosum*; (c) cyanolichen *Peltula richardsii*; (d) cyanolichen *Peltula patellata*.

Source: From Büdel et al. (2013). With kind permission of Springer.

Under dry antecedent conditions, about half the water ran off those plots with the lowest level of development of the biological soil crust while only 10% ran off the plots with the highest level of development. Büdel et al. (2013) tested the photosynthetic abilities of soil crust in the Sonoran Desert of Baja California (Mexico) on two dominating chlorolichens *Psora decipiens* and *Placidium squamulosum* and the cyanolichens *Peltula patellata* and *Peltula richardsii*. The chlorolichen biological soil crusts exhibited positive net photosynthesis under conditions of high air humidity alone, while the cyanolichen types did not. However, the cyanolichens displayed less CO_2-uptake depression after water suprasaturation. Such specific net photosynthesis responses to mode of hydration and to crust water content appeared to correlate with precipitation characteristics of their habitat, as was recorded by Belnap et al. (2013).

3.4 Annual plants

Annual plants live for one growing season or year and then survive until the following growing season as seeds. Smith et al. (1997) emphasized that desert annuals have little capacity for photosynthetic acclimation, unlike evergreen species, and are unable to handle severe drought. Some annuals are amphiphytic, that is, they may be annual or perennial depending on local environmental conditions (Orshan 1986; Danin 1996). For example, several species of the grass genus *Stipagrostis* (e.g. *Stipagrostis plumosa, Stipagrostis ciliata*, and *Stipagrostis hirtigluma*) are perennial under moderate conditions but are annual when conditions become more extreme (Danin 1996). A few species of *Fagonia* are also capable of this behaviour (Orshan 1986).

3.4.1 Desert versus mesic annual species

An effective way to establish the nature of adaptations is to make comparisons among congenerics or among races or populations of the same species. For example, *Machaeranthera gracilis* (Asteraceae) has both desert and foothills races in the Sonoran Desert. The foothills race occurs in cooler and wetter pinyon-juniper and ponderosa pine woodlands and the desert race in the hotter and drier lowlands (Jackson and Crovello 1971). Plants of the desert race have higher photosynthetic rates than the foothills race, reach anthesis sooner after germinating, and allocate more biomass to reproduction (Anderson and Szarek 1981; Monson and Szarek 1981). Studies of conspecific desert and Mediterranean populations of several annual species (*Erucaria hispanica, Brachypodium distachyon, Bromus fasciculatus* and *Hordeum spontaneum* (wild barley), *Triticum dicoccoides* (wild emmer wheat), and *Avena sterilis* (wild oats)) demonstrate patterns similar to those observed in *Machaeranthera gracilis*, with accelerated growth rates in desert forms compared with Mediterranean plants (Nevo et al. 1984; Volis et al. 2004; Volis 2007). Desert populations exhibit greater sensitivity to late-season water stresses and have greater seed set and senescence of vegetative growth, resulting in higher reproductive allocation (Owuor et al. 1999; Volis et al. 2004). Volis (2007) found that both *Hordeum spontaneum* and *Avena sterilis* had earlier onset of flowering and produced more seeds that were smaller at the arid end of the rainfall gradient than at the Mediterranean end of the gradient. Similarly, more seeds per plant but of smaller size were also observed in the desert as compared with the Mediterranean population of an annual grass, *Stipa capensis* (Aronson et al. 1990). These findings emphasize the importance of seed size as part of a plant's reproductive strategy (Leishman and Westoby 1994; Westoby 1999). The initial seedling size is positively correlated with seed size (Leishman et al. 2000). Although larger initial seedling size may be advantageous under competition or drought (Leishman and Westoby 1994), large seed size may trade off with lower persistence in the seed bank due to seed predation (Gutterman 2002).

3.4.2 Seed germination and dispersal strategies

Some of the most unique adaptations of desert organisms involve dispersal by plants (reviewed by Van Rheede van Oudtshoorn and Van Rooyen 1999; Gutterman 2000, 2002) (see Fig. 3.6; see also Stamp 1984). One of the most interesting and sophisticated mechanisms of dispersal involves the ice plants, Mesembryanthema (Aizoaceae). Harrington et al. (2011) investigated the hydration dependence of unfolding in ice plant capsules (specifically in *Delosperma nakurense*). They found that there was a reversible folding pattern that works by means of a cooperative flexing-and-packing

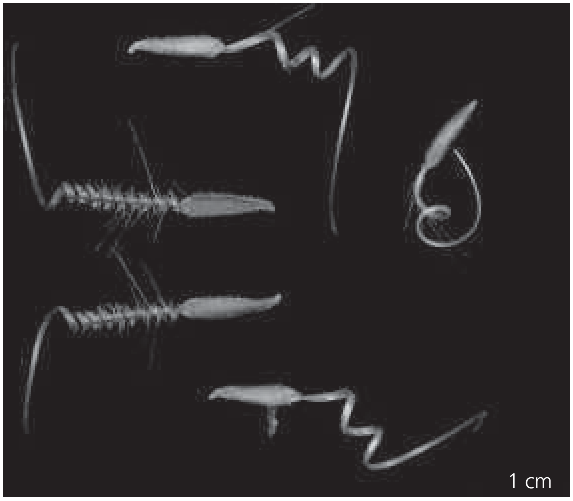

Fig. 3.6 *Erodium cicutarium* seed dispersal.
Source: Photo by Didier Descouens (Museum of Toulouse, France) under Creative Commons licence.

mechanism that is initiated by a swellable cellulose layer that fills specialized plant cells. Swelling translates into a bidirectional movement that is constrained in a simple geometric way that is embedded in the hierarchical architecture of the valves of the ice plant (Figs. 3.7 and 3.8).

Gutterman (1994) indicated that there are two main strategies of dispersal to avoid massive seed consumption, a common problem in plants that reproduce annually and need to survive in the seed stage until the following year:

1 *Escape strategy*—seeds escape by being very small. For example, *Schismus arabicus* can produce 10,000 caryopses (seeds) per square metre, each weighing an average of 0.007 mg. *Spergularia diandra* may produce as many as 32,000 seeds per square metre, each weighing 0.018 mg.
2 *Protection strategy*—There are a number of different ways to protect a seed. For example, seeds could be maintained on the parent plant where it is covered by woody and/or dry material. Examples of this include the amphicarpous (two or more ways of preserving seeds) *Gymnarrhena micrantha* and *Emex spinosa* (Polygonaceae). Serotiny (preservation within a woody structure; also called bradyspory *sensu*; Van Rheede Van Oudtshoorn and Van Rooyen (1999)) has been shown in a number of Namib Desert plants (Günster 1992, 1993a, b) and in Negev Desert plants (e.g. in *Asteriscus pygmaeus* (Asteraceae) by Gutterman and Ginott (1994)). However, Günster (1994c) has challenged the notion that the protection of seeds of serotinous (bradysporic) plants is a driving force in the evolution of these species because she found no difference in insect predation of serotinous and non-serotinous plants. Some plants are protected by myxospermy, which means that they are covered with a layer of mucilage

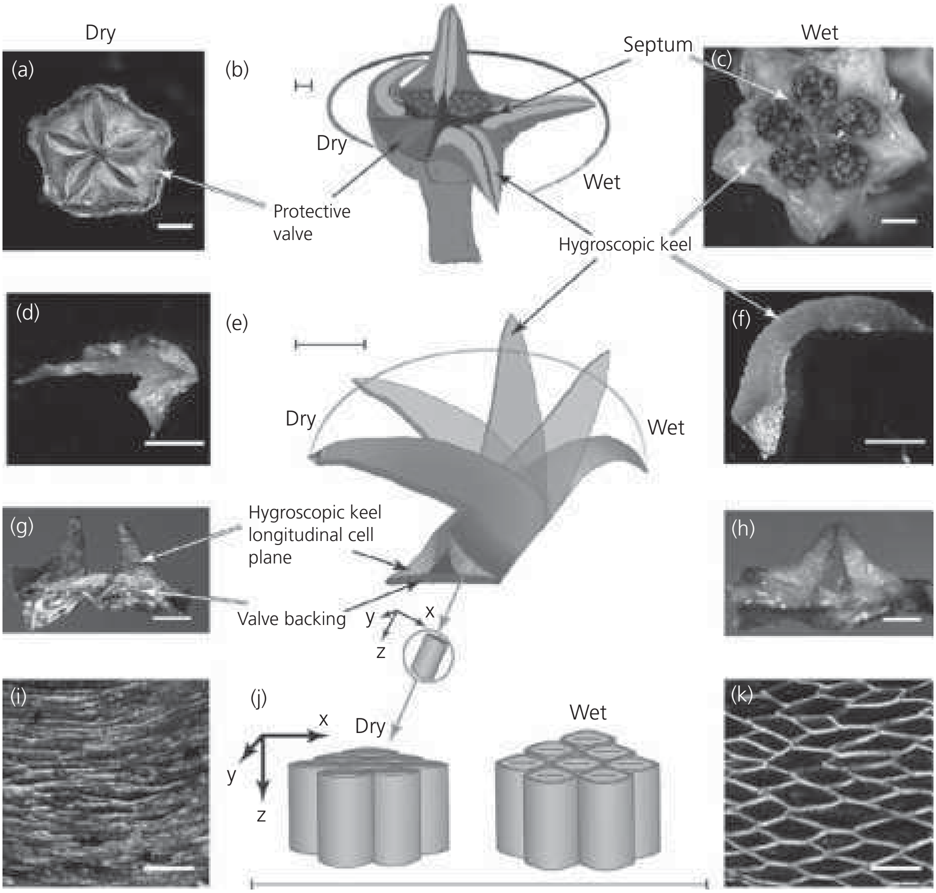

Fig. 3.7 Light and confocal microscopy images depict the morphology of the ice plant capsule and the hygroscopic keel tissue at different hierarchical levels (a–k). For each hierarchical level, an illustrated schematic provides a simplified representation of structures and the progressive movements that occur during water-dependent actuation. Scale bars are defined as follows: (a, c) 2 mm; (b, d–f, j) 1 mm; (g, h) 0.5 mm; (i, k) 0.1 mm.

Source: From Harrington et al. (2011).

and then attach themselves to the biological soil crust to avoid ant herbivory. Examples of such plants include *Plantago coronopus*, *Carrichtera annua* (Fig. 3.9), and *Reboudia pinnata* (Gutterman and Shem Tov 1997). However, Zaady et al. (1997) found that seeds of these species did not germinate well under such conditions and rather need the soil crust to be broken up. Thus, it may be that avoiding ant herbivory is necessary for the seeds to endure the (dry) summer but breaking up the soil crust must occur the following (wet) winter for these winter annuals to germinate. Zaady et al. (1997) speculate that this may explain why germination occurs best when the seeds occur in the

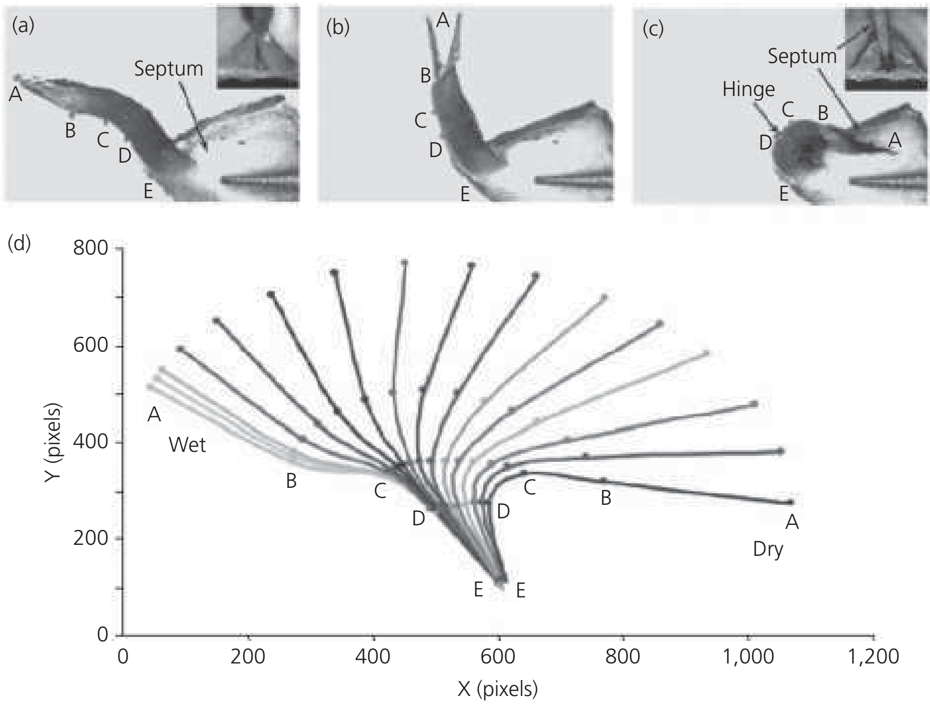

Fig. 3.8 Detailed analysis of keel movement in an ice plant. Image correlation was used to track the movement of a dissected keel during drying. A keel attached to the septum with the backing dissected away can be seen in the wet state. (a) An intermediate state. (b) The dry state. (c) The spots labelled A–E were followed in consecutive frames to observe the relative movements of the keel. Insets (a, c) show the tight packing of the keel around the septum in the dry state. (d) Plot of relative movements of points A–E during drying.

Source: From Harrington et al. (2011).

shallow holes formed by porcupine (*Hystrix indica*) diggings, which frees the seeds of attachment by their mucilage.

3.4.3 Why is long-range dispersal rare in desert plants?

Many authors have observed that there are few species of desert plants that show adaptations for long-distance dispersal (Zohary 1937). For example, Venable et al. (2008) found that seeds of most desert annuals in the Sonoran Desert of North America disperse less than 1 m. One explanation has dominated with regard to the dispersal of desert plants, namely, the 'mother-site' theory of Zohary (1937). Consistent with Zohary's theory, Friedman and Stein (1980) contend that in deserts, where the number of suitable sites is limited, a plant that occupies the place that once supported its mother is likely to have a good chance of success. This assumes that competition is rare in deserts and that the benefits of germinating in a particular

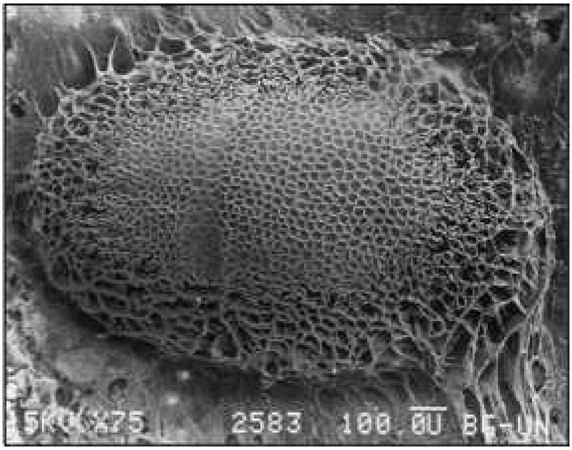

Fig. 3.9 *Carrichtera annua* seed with mucilage (upper section) to attach itself to loess.
Source: From Gutterman (1993). With kind permission of Springer.

site outweigh any purported costs. Such a theory may explain why adaptations for long-distance dispersal (*telechory*) are rare in desert plants. Two terms have been derived to describe adaptations associated with dispersal, namely, atelechory and antitelechory. Atelechory entails a lack of adaptations for dispersal and antitelechory describes adaptations to prevent dispersal (Zohary 1937).

Ellner and Shmida (1981) have contested the mother-site theory, although they do acknowledge that there are few adaptations for long-distance dispersal in desert plants (Tables 3.2 and 3.3). Ellner and Shmida (1981) argue that annuals do not rely on special moist microsites as they can be widely distributed across the desert in moist years. They also note that geocarpy and amphicarpy, which are adaptations to retain seeds in the same site, are rare or absent in deserts. Furthermore, fine-scale spatial distributions should be common among years but are not. Indeed, these authors show that their small 10 × 10 cm plots in the Judean desert have a relatively high temporal variance (0–66% similarity). This has also been shown by Ward et al. (2000a) on a larger spatial scale (0.1 ha) in the neighbouring Negev Desert, where plants mostly have a <10% probability of appearing more than once in the same plot (see Fig. 7.1). Ellner and Shmida (1981) name five possible reasons, excluding the mother-site theory, why antitelechory might have evolved:

1. *Protection from predation*—consistent with Gutterman's (1994) model mentioned earlier, buried seeds and/or seeds attached to the mother plant are less likely to suffer from seed predation.
2. *Anchorage against surface run-off*—this is particularly important for slope-dwelling species because they may get washed into the wadis, even without specialized mechanisms for dispersal.

Table 3.2 Major dispersal types of the Israeli flora

Dispersal type	Mediterranean/ semi-desert	Desert	Sansan (open maquis)	Ein Gedi (desert)
Telechory	41.6 (574)	14.6 (88)	45.0	26.0
Atelechory	56.6 (780)	75.0 (453)	53.0	52.0
Antitelechory	1.8 (25)	10.4 (62)	2.0	22.0

Note: The columns indicate the % of species with a particular dispersal type (numbers in parentheses indicate number of species involved). Columns 4 and 5 indicate the dispersal types of total numbers of species counted in 0.1-ha plots at a single site in 1980 (Sansan) and 1981 (Ein Gedi). Percentages of species have been recalculated for Mediterranean/semi-desert based on numbers of species with a particular dispersal type from Ellner and Shmida (1981).

Source: Modified from Ellner and Shmida (1981).

Table 3.3 Dispersal types of the Goegap nature reserve in arid Namaqualand, South Africa

Dispersal type	Goegap
Telechory	47.6 (736)
Atelechory	8.1 (126)
Antitelechory	44.3 (685)

Note: Numbers indicate the % of species with a particular dispersal type. Numbers in parentheses indicate the numbers of species involved. Note the difference in % values for atelechory and antitelechory for this study and the one mentioned by Ellner and Shmida (1981) (Table 3.2).

Source: From Van Rheede Van Oudtshoorn and Van Rooyen (1999).

3. *Regulation of within-season timing of germination*—precipitation occurs rarely in deserts, so germination should be timed to coincide with these events.
4. *Spreading dispersal and germination over several years*—responses to early season rains can lead to high mortality if not followed by subsequent rains (Loria and Noy-Meir 1981). Selection should favour multiple germination events in the same species (*polyphenism*) (Cohen 1966, 1967).
5. *Enhancing water uptake by seeds and seedlings*—seeds that are buried in the soil can have reduced exposure to extreme heat and cold and have better access to water than unburied seeds.

Ellner and Shmida (1981) contend that atelechory has evolved because of the extremely low benefit to be derived from long-distance dispersal (i.e. possession of morphological features such as pappi and barbs; Fig. 3.10) rather than a benefit of adaptive short-range dispersal. They suggested that antitelechory, on the other hand, is part of a group of characteristics that happen to have evolved for the purpose of regulation of the timing of germination to limit it to years after the mother plant has died. It is important to note that the mother-site theory of Zohary (1937) and Ellner and Shmida's (1981) theories are not mutually exclusive.

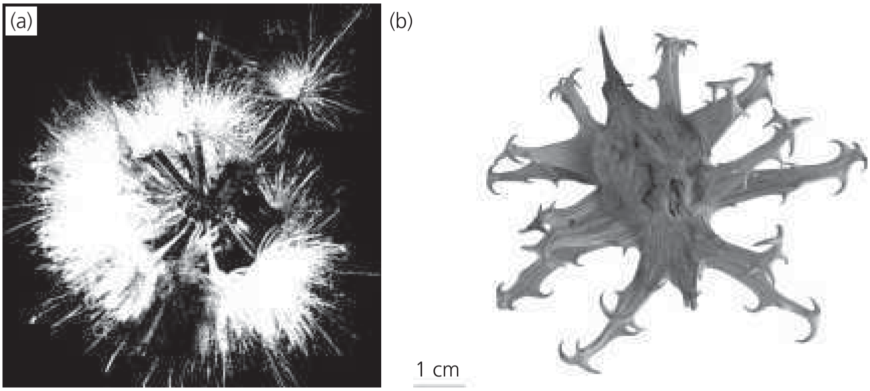

Fig. 3.10 (a) Pappi of a dandelion and (b) barbs (in African devil's claw *Harpagophytum procumbens*) used as dispersal mechanisms.

Source: Photo of Y. Gutterman (a) and Roger Culos under Creative Commons licence (b).

3.4.4 Delayed germination

Cohen (1967) addressed the question of why annual plants have delayed germination. Using mathematical models, he showed that the higher the probability of seed failure following a rain event, the smaller the optimal germinating fraction should be. Venable et al. (1993) found support for this model in the Sonoran Desert, where each of the 10 species they studied had a greater germinating fraction in years of greater germination success (see also Adondakis and Venable 2004). A mechanism that could give rise to such a pattern could be as simple as having a germination fraction sensitive to conditions favourable for early growth and establishment (Van Rheede van Oudtshoorn and Van Rooyen 1999). Weather data at a local weather station in Arizona over the past 115 years indicated a significant correlation between December rainfall (a good predictor of germinating fraction) and February rainfall (a good predictor of realized fecundity) (Venable et al. 1993).

3.4.5 Seed heteromorphism

Seed heteromorphism is known in a number of deserts, including the Arabian Desert (*Emex spinosa* (Weiss 1980) and *Gymnarrhena micrantha*; Koller and Roth 1964), Namib Desert (e.g. *Geigeria alata*; Burke 1995), Sonoran Desert (*Heterotheca pinnatum*; Venable et al. 1995), and Junggar Desert of China (*Diptychocarpus strictus*; Lu et al. 2010). The strategy of such plants is to invest simultaneously in two or more types of seeds. In *Emex spinosa*, for example, one seed type is aerial and the other is subterranean. Aerial seeds are dispersed greater distances by wind, while subterranean seeds are dispersed locally (Weiss 1980). In *Diptychocarpus strictus*, there are two flower colour morphs (purple and white) and two morphologically distinct types of fruits (called upper and lower siliques, which are two fused carpels) are produced by each of them (Lu et al. 2010). Additionally, seeds from upper and lower siliques of each flower colour morph vary in width of the wing and in amount of mucilage. Siliques and/or seeds are dispersed within a few days after maturity by wind or rain. The seeds with a wide wing from the upper siliques are the units of dispersal and of germination. However, lower siliques with highly lignified pericarps do not dehisce and are usually dispersed near the mother plant. In most cases, local dispersal is more effective because there is little benefit to leaving an area that was successful for the mother plant for another area that may or may not be better (*sensu* Zohary 1937, 1962).

Venable (1985) developed a game theory model to consider the issue of seed heteromorphism and its effects on fecundity. The appropriate method of comparing fecundity is by the geometric mean (the *n*th root of the product of *n* values) and not by the arithmetic mean (sum of the numbers divided by *n*), because the geometric mean controls for very high or very low values. In the case of annual seed yields, the geometric mean can be increased by increasing the arithmetic mean seed yield or by reducing the variance (Gillespie 1977). Only one seed type is necessary to maximize the arithmetic mean but two morphs can reduce the variance. For example, there are two seed types and they have respective annual seed yields of 2, 5, and 8 seeds (morph 1) and 8, 5, and 2 seeds (morph 2). If the seed types represent different strategies and all seeds germinate and survive to reproduce, there will be 80 descendants of a single individual after 3 years ($2 \times 5 \times 8 = 80$ seeds). If they are morphs in a 1:1 ratio with a heteromorphic strategy, the arithmetic mean offspring fitness is 5 seeds per annum (arithmetic mean of 2, 5, and 8 = 5) or 125 seeds over three years. All strategies have a mean arithmetic yield of 5 seeds per annum but the heteromorphic strategy has the highest yield because they have a lower between-year variance (Venable 1985).

Venable (2007) has also addressed the notion of bet hedging in desert annuals. Bet hedging involves trading off short-term geometric mean fitness for long-term risk reduction. Using the 10 most common species in a 22-year study near Tucson, Arizona, Venable (2007) found that bet hedging does indeed occur; there was a significant negative correlation between the log-transformed standard deviation (SD) and mean germination fraction (Fig. 3.11).

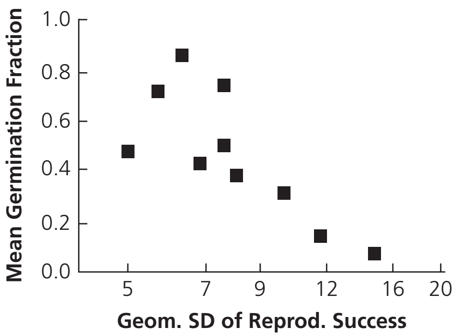

Fig. 3.11 Mean germination fraction of 10 species of desert annuals plotted against variation in per capita reproductive success (average number of germinating seeds). Germination is averaged over 14 years. Demographic variation is calculated over 22 years and is plotted as geometric SD (exp. SD [ln (per capita reproductive success)]).

Source: Modified from Venable (2007). With the kind permission of the Ecological Society of America.

3.5 Grasses, forbs, and shrubs/perennials

3.5.1 Clonality

Vasek (1980) showed that creosote bushes *Larrea tridentata* (Zygophyllaceae) are clonal and are extremely long-lived. The oldest known *Larrea* occurred in Yuma, Arizona, occurred there about 10,850 ± 500 years BP. Assuming that the growth rate was 0.66 mm yr^{-1} from about 7,000 years ago and was double that prior to 7,000 BP, this would indicate that such a shrub would be at least 9,400 years old.

Bruelheide et al. (2004) have shown that clones of *Populus euphratica* in the Taklamakan Desert can be larger than 100 m in radius, leading to a calculation of at least 4 ha occupied by a single clone, yet a perennial herb *Alhagi sparsifolia* (Fabaceae) sampled at the same site had clones that were > 5 m but < 100 m radius. Bruelheide et al. (2004) note that *Populus euphratica* may even have clones that are > 4 ha in spatial extent because no further spatial sampling was conducted.

3.5.2 Photosynthesis and stomatal opening

Kappen et al. (1976) showed in the drought-deciduous shrub *Hammada scoparia* (Chenopodiaceae) in the Negev Desert that non-irrigated plants on hillslopes had a net photosynthetic rate of approximately 3 mg CO_2 g^{-1} h^{-1}, while non-irrigated wadi plants had a net photosynthetic rate of about 5 mg CO_2 g^{-1} h^{-1}. In contrast, irrigated wadi plants had a value of about 7 mg CO_2 g^{-1} h^{-1}. The mean midday water potentials of these same plants were −7 MPa (going as low as −9.1 MPa (−91 bars)), −7 MPa, and −5 MPa, respectively. Kappen et al. (1976) contended that the relatively high net rate of photosynthesis in mid-summer (July) occurred even under low (i.e. very negative) water potentials. These results may be explained by the fact that

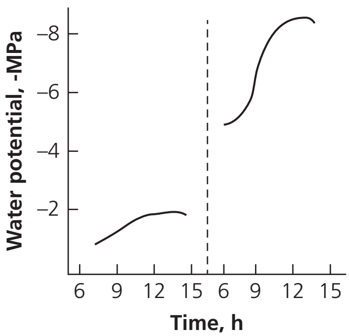

Fig. 3.12 Photosynthesis can be achieved even under extreme water stress conditions: Halvorson and Patten (1974) recorded a water potential of −8.5 MPa in *Franseria deltoidea.*

Source: From Halvorson and Patten (1974). With the kind permission of the Ecological Society of America.

wadi plants have a prolonged period with less sensitive stomata in summer unlike the hillslope plants which had been under high water stress since spring (because hillslope plants occur where run-off is high and wadi plants occur where run-on is highest). This may lead to permanently low water potentials and low rates of net photosynthesis, resulting in the shedding of the plant's cortex in the wadis by the end of the dry season, and hence deciduousness (Kappen et al. 1976).

More extreme values of xylem and leaf water potential have been recorded at−16.3 and −9.2 MPa by Kappen et al. (1972) in *Artemisia herba-alba*, also in the Negev Desert. These values produced a low but nonetheless positive value of net photosynthesis of about 0.2 mg CO_2 g^{-1} h^{-1}. Similar values have been recorded for desert shrubs by Halvorson and Patten (1974), who recorded a water potential of −8.5 MPa in *Franseria deltoidea* (Fig. 3.12) in the Sonoran Desert at noon. Before sunrise and after sunset, the values for Kappen et al.'s (1972) study on *Artemisia herba-alba* were still very negative, being around −10 MPa for xylem and −5 MPa for the leaves. Donovan et al. (2001) have indicated that soil and leaf water predawn potentials may not equilibrate because either night-time transpiration or apoplastic solute transport occurs (or both). Nonetheless, they can account for relatively small predawn disequilibria between soil water potentials and leaf water potentials of about −0.5 to −2.34 MPa in bagged plants that cannot transpire (Donovan et al. 2001). Values as extreme as those in *Artemisia herba-alba* are difficult to explain.

3.5.3 Heat shock proteins

There have been considerable advances over the past 30 years in our understanding of heat shock proteins and their functions at the biochemical, physiological, and ecological levels (Ackerly et al. 2000; Al-Whaibi 2011). The induction of transcription of these proteins is a common phenomenon in all living things. These proteins are grouped in plants into five classes according to their approximate molecular weight

(Al-Whaibi 2011). Most important in higher plants are small heat shock proteins (sHSPs). Higher plants have at least 20 sHSPs and there might be 40 kinds of these sHSPs in a single plant species. It is likely that the diversification of these proteins reflects an adaptation to tolerate heat stress (Al-Whaibi 2011).

The low molecular weight heat shock protein (lmw HSP) genes are located in the nucleus, and in response to stress, the proteins are synthesized and transferred to the chloroplast and mitochondria. Heckathorn et al. (1998) isolated chloroplasts, so that the nuclear-encoded proteins could not be synthesized, and exposed them to heat shock. In the absence of the lmw HSPs, photosystem II experienced heat damage and electron transport levels declined. The subsequent addition of purified HSP rapidly restored photosynthetic activity, demonstrating that these HSPs protect the electron transport chain from damage and may contribute to repair of damaged photosystem proteins.

The C_3 plant *Rhazya stricta* occurs in the hyperarid Arabian Desert with a mean annual rainfall of only 45 mm. The Lawson et al. (2014) study linked *Rhazya stricta*'s ecophysiological features to HSPs. Lobell et al. (2012) had found that high temperatures and heat stress are often coupled with water stress. As vapour pressure deficit (VPD) increases there is increased evaporative cooling and transpiration (Lobell et al. 2013). Stomata need to balance demands for CO_2 uptake with transpirational water loss to use water efficiently (Wong et al. 1979; Pearcy 1990; Lawson et al. 2010). Lawson et al. (2014) observed the uncoupling of assimilation (A) and stomatal conductance (g_s) in *Rhazya stricta* at particular times during the day (Fig. 3.13). They found that there was an early morning peak in stomatal conductance (Fig. 3.13b), which is considerably higher than necessary for photosynthesis at that incident photosynthetically active radiation (PAR). This was likely to have been driven by the plant's need for evaporative cooling to maintain a lower leaf temperature (Lobell et al. 2013). This confirms that *Rhazya stricta* is not water stressed (because it has sufficient water to evaporate). Plants functioning at high temperatures also need to respond to the effect of heat stress on carbon metabolism. This is generally believed to be the primary limiting factor for photosynthesis at high temperatures (Kurek et al. 2007). This may act directly and indirectly. Temperature directly affects the activity of several Calvin cycle enzymes, with attention focused most on Rubisco activase (RCA; Parry et al. 2003; Galmes et al. 2013). Indirect effects of temperature on stomatal conductance and photorespiration reduce carbon assimilation. Lawson et al. (2014) took ecophysiological measurements on *Rhazya stricta* in conjunction with gene expression analysis. They found that there were two isoforms of RCA, indicating that *Rhazya stricta* can maintain Rubisco function at high temperatures.

Variation in patterns of HSP production may help explain the evolution of broad variation in thermotolerance among plant species. Some evidence suggests that thermotolerant species such as desert cacti allocate a far greater proportion (several orders of magnitude) of leaf protein to chloroplast HSPs than do thermosensitive species (Downs et al. 1998). The relative allocation of protein to chloroplast HSPs is also highly correlated with photosynthetic thermotolerance of populations of the annual plant species *Chenopodium album* (Heckathorn et al. 1999)

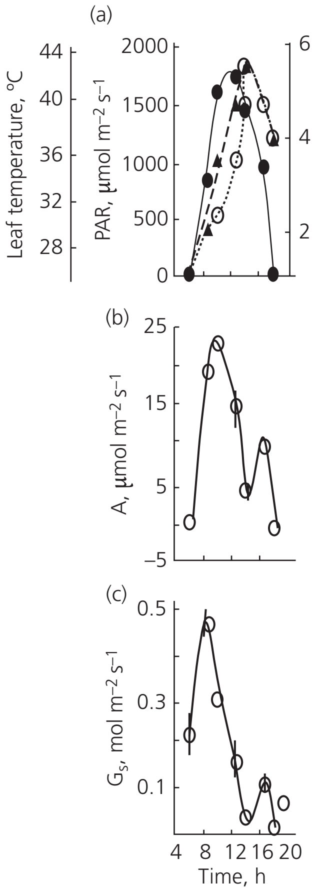

Fig. 3.13 Diurnal measurements in *Rhazya stricta*, a C_3 plant from the hyperarid Arabian Desert. (a) Photosynthetically active radiation (PAR; closed circles), leaf temperature (triangles), vapour pressure deficit (VPD; open symbols); (b) net CO_2 assimilation (*A*); (c) stomatal conductance to water (G_s).

Source: Modified from Lawson et al. (2014). With kind permission of The New Phytologist Trust.

and species of the perennial shrub genus *Ceanothus* (Knight and Ackerly 2001). There is a strong positive correlation between chloroplast HSP production and thermotolerance, and all plants that have been tested have the machinery to make chloroplast HSPs (Ackerly et al. 2000). This begs the question 'Why do all plants not produce large quantities of HSPs, conferring greater thermotolerance?' One possibility is that production of chloroplast HSPs is physiologically costly in terms of their nitrogen requirement; nitrogen limitation reduces the relative allocation of protein to chloroplast HSPs in maize/corn *Zea mays* and tomato *Solanum lycopersicum* and reduces photosynthetic thermotolerance (Heckathorn et al. 1996).

Together, these results suggest that although HSPs may be required for physiological function, especially in the presence of heat shock and other stresses, variation in their production may reflect trade-offs in allocation of protein between HSPs and photosynthetic proteins, and optimization of the benefits of thermotolerance with the physiological costs of HSP production (Ackerly et al. 2000). Because of the detailed work on the molecular biology of HSPs, their conservation throughout plant evolution, and their significance with respect to plant tolerance of environmental stresses, HSPs represent a model trait for the study of optimizing selection and ecophysiological evolution (Ackerly et al. 2000).

3.5.4 Specific leaf area

Knight and Ackerly (2003) found support for the hypothesis that reduced specific leaf area (SLA) is a convergent trait in plant lineages evolving into thermally stressful environments with lower annual precipitation such as deserts. Their results, like other studies, indicate that, within the same habitat, variation among species for SLA is considerable, reflecting the diversity of growth strategies and life histories within the same community (Reich et al. 1997; Ackerly et al. 2000; Ackerly 2003). The reduction in SLA in the desert primarily represents an absence of species with high SLA; there were species with low SLA at the coastal field site (e.g. *Eriogonum latifolium*) but species at the coastal field site also had the greatest SLA (e.g. *Encelia californica*).

Leaves with lower SLA were better able to withstand and recover photosynthetic electron transport after high temperature stresses than species with greater SLA (Fig. 3.14a). In the field this correlation was apparent for all species pairs as well as across all taxa (paired and unpaired). When grown in a constant environment, the correlation was not robust within congeneric pairs because of the lack of genetic variation for photosynthetic thermal tolerance, but there was a negative trend (Fig. 3.14b). Knight and Ackerly (2003) found that, after identical heat stresses, species with lower SLA accumulated greater levels of a chloroplast small heat shock proteins (sHSP) compared to species with higher SLA. Other studies suggest that greater leaf longevity, which is associated with low SLA (Reich et al. 1997), promotes nutrient retention, enhancing long-term photosynthetic nitrogen-use efficiency (Field and Mooney 1986; Chapin et al. 1993). Resilience to thermal damage of photosynthetic mechanisms is likely to occur in species with low SLA, i.e. species with leaves that demonstrate their tolerance of stresses.

3.5.5 Leaf pubescence

Sandquist and Ehleringer (1998) studied reflective leaf pubescence in a desert shrub, *Encelia farinosa* in the Sonoran Desert. Leaf hairs have high (albeit once-off) construction costs and reduce photosynthetic efficiency by cutting down on photosynthetically active radiation (PAR). However, leaf pubescence reduces leaf

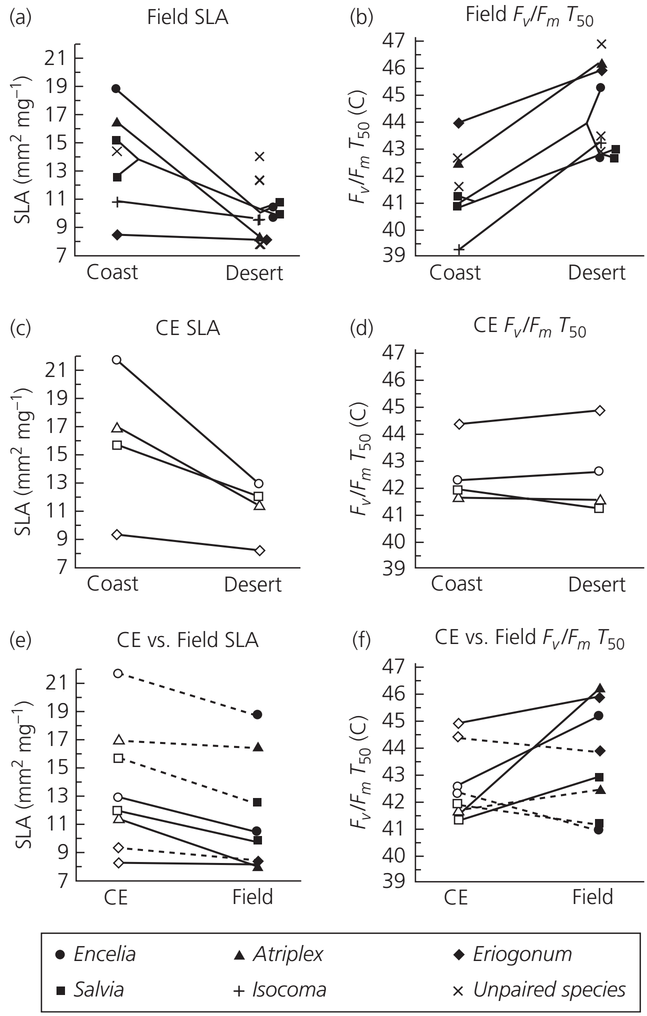

Fig. 3.14 Differences between congeneric species at Mojave Desert and coastal (near Santa Barbara, CA, U.S.A.) sites for (a) SLA and (b) F_v/F_m (= temperature-dependent decline in the photochemical efficiency of photosystem II (PSII), quantified as the ratio of variable to maximal fluorescence. Congeneric species are connected by solid lines. There were two *Salvia* and two *Encelia* species at the desert site and two *Salvia* species at the coastal site. The means of these pairs are connected to the congener/s in the opposite environment by a solid line. Unpaired species are represented by an X. Genetic differences for (c) SLA and (d) F_v/F_m are represented in the common environment (CE). Plasticity for (e) SLA and (f) F_v/F_m are represented for the CE and the field sites. Measurements in the CE are represented by open symbols and measurements in the field are represented by closed symbols. Dashed lines connect measurements for the coastal species between the CE and field in (e) and (f).

Source: Modified from Knight and Ackerly (2003). With kind permission of the University of Chicago Press.

temperature and plant water loss and is therefore considered adaptive in arid environments. Using three sites along a natural rainfall gradient, with mean rainfall values at 52, 111, and 453 mm per year, Sandquist and Ehleringer (1998) showed that drought-induced leaf loss was earliest at the high rainfall site but these plants also had higher leaf absorbance values. Higher absorbance increases the relative dependence on transpirational cooling and, perhaps more importantly, also allows for higher instantaneous carbon assimilation. Conversely, plants at the driest site had lower absorbance values and maintained their leaves for longer. Lower absorbance values, which are associated with greater leaf pubescence, reduced water consumption. These studies showed that a trade-off exists between carbon assimilation (wetter sites) and reduced water consumption. Plants from drier sites may also need to extend leaf longevity to maintain photosynthetic activity for longer into the dry season.

3.5.6 Fog—an unusual water source

Two plant species in the Namib Desert, *Trianthema hereroensis* (Aizoaceae) and *Stipagrostis sabulicola* (Poaceae), are capable of using fog, at least as a supplementary source of water (Louw and Seely 1980). Using tritiated water (a commonly used tracer for water transport studies, where the hydrogen ions are replaced with tritium; the chemical formula is ^3H_2O), they showed that the succulent *Trianthema hereroensis* can take up large amounts of this water sprayed on its leaves, indicating that they can use fog water in the same way (Seely et al. 1977). This strategy is unlikely to be effective because water taken up by the leaves is even more likely to evaporate from the leaves (Von Willert et al. 1992). However, the perennial grass *Stipagrostis sabulicola* has an extensive superficial root system, part of which lies within 1 cm of the substrate. This sand layer is often moistened with fog. Louw and Seely (1980) showed that when moistened to field capacity with tritiated water, this water was taken up by these roots. When the same plants were tested 7 weeks later, most of the photosynthates were transferred to the main vertical and lateral roots.

3.5.7 Grasses

Most species of plants in deserts are grasses (see Chapter 9). Grasses are usually C_4 species and show many of the classic adaptations of such plants (see section 3.2, ‘Types of photosynthesis’).

The distinctive Australian hummock grasslands consist largely of grasses of two genera, *Triodia* and *Plectrachne* (often called desert spinifex). The hummocks can be large, up to 1 m in diameter and about 30 cm tall (Specht and Specht 1999). The hummock grows outwards, leaving the centre senescent or dead. Hummock grasses typically occur where mean annual rainfall is between 125 and 350 mm. Unlike many other desert situations, where there is usually insufficient fuel for a fire, these Australian hummock grasslands are prone to fire.

Ryel et al. (1994) examined the factors that may lead to hummock or tussock formation (also called bunch grasses), a common desert grass formation. Tussock grasses are composed of essentially autonomous tillers (Welker et al. 1991). They compared the physiology of uniform tillers with those of bunch grasses of *Agropyron desertorum*, in the Great Basin Desert of North America. When tussock density was low, they found that bunch grasses had 50–60% lower carbon gain, lower daily incident photon flux density, and lower net photosynthesis than equivalent uniformly distributed tillers because of light competition within tussocks. When tussock densities were high, they found that there was considerable variability in net photosynthesis, ranging from 7 to 96% relative to an isolated seedling. Ryel et al. (1994) hypothesized that the loss of net photosynthesis because of clumping is offset by the benefits of protecting their below-ground resources from competing seedlings.

3.6 Geophytes

The term 'geophyte' refers to plants that use underground organs for storage. Most plants in this category belong to the monocot families Iridaceae, Liliaceae, and Amaryllidaceae. Various types of storage organ can be considered, including bulbs, corms, rhizomes, and, in some cases, tubers. True bulbs, if cut in half vertically, reveal the components you would find in a bud, namely, flower and leaves (Fig. 3.15). Examples of true bulbs include tulips, lilies, and narcissus. Alternatively, corms are solid, enlarged stem bases, such as anemones and crocus. Rhizomes are swollen stems that grow horizontally typically underground and send up leaves and flowers at intervals.

Fig. 3.15 Geophytes, *Pancratium sickenbergeri*, from the Negev Desert, Israel.

Irises are the best-known rhizomes. The term 'tuber' is applied to any plant with underground storage parts that does not fit these other categories.

3.6.1 Hysteranthy and its consequences

Hysteranthous plants produce their flowers at different times from their leaves while synanthous plants produce flowers and leaves simultaneously. In Israel, only a few plant species flower in the autumn (about 10% of the native flora; Zohary 1962). Most of them are hysteranthous geophytes. Dafni et al. (1981) have claimed that these species have adopted a new pollination strategy that avoids the conventional timing of pollination in the spring and thus avoids 'arms races' with other potential pollinators. However, Kamenetsky and Gutterman (1994) have shown that these hysteranthous plants may retain their seeds for several months, even as late as January the following year, and thereby avoid ant predation, which is a major source of seed predation. Clearly, the pollination and seed predation-avoidance strategies are not necessarily mutually exclusive.

Boeken (1989, 1990) investigated the consequences of hysteranthy for two species in the genus *Bellevalia* (Hyacinthaceae (Dahlgren et al. 1985), or, alternatively, Liliaceae (Cronquist 1981) or Asparagaceae (Angiosperm Phylogeny Group 2003)) growing in the central Negev Desert of Israel. Boeken (1989) showed that the reproductive state of a population of *Bellevalia desertorum* was determined by the size of the plant and by the current conditions (rainfall) but not by previous conditions or previous reproductive activity. In contrast, he showed that *Bellevalia eigii* was affected by previous and current conditions and found that there was a negative effect of previous reproduction (Boeken 1990). In a study of *Pancratium sickenbergeri* (Amaryllidaceae), Ward et al. (2000a) found a significant positive effect of rainfall in the previous season but none from the current season.

3.7 Stem and leaf succulents

This category may be divided into two non-phylogenetically related groups of organisms, stem succulents (such as the Cactaceae and Euphorbiaceae species) and leaf succulents (such as *Lithops* and *Aloe*). Many succulents have CAM photosynthesis. However, this is not universally true (see Von Willert et al. 1982).

3.7.1 Stem succulents

Here we consider three examples of stem succulent life histories.

3.7.1.1 Welwitschia mirabilis (Gnetales, Gymnospermae)

Unlike most desert succulents, this species is a gymnosperm that is endemic to the narrow coastal strip of the Namib Desert (Fig. 3.16). Schulze and Schulze (1976) have

Fig. 3.16 *Welwitschia mirabilis*, Namib Desert, Namibia.
Source: Photo courtesy of Megan Griffiths.

considered this species to be capable of CAM photosynthesis on the basis of carbon isotope values. However, Von Willert et al. (1982) re-examined this in the field and have not found any evidence to support this claim. Von Willert et al. (1982) argue that this species has conventional C_3 photosynthesis. No evidence of nocturnal CO_2 uptake (as expected from CAM photosynthesis) was detected. Nonetheless, fairly high values of malate and citrate were found in the leaves of this plant (as expected with CAM photosynthesis), yet these did not exhibit any diurnal–nocturnal pattern. Von Willert et al. (1982) found that transpiration rates (to a maximum of 1.9 mmol m^{-2} s^{-1} near 12h00) occurred, which would imply that about 25–32% replacement of leaf water loss per *hour* should occur. It is unclear as to where this is obtained, although it is suggested that the woody trunk, which is sponge-like, may serve as a water store.

3.7.1.2 Ferocactus (Cactaceae)

As indicated by their common name of 'barrel cactus', *Ferocactus* are roughly spherical in morphology (Fig. 3.17). These dicotyledonous plants use CAM photosynthesis. Succulent plants generally have a thick chlorenchyma, which in *Ferocactus cylindraceus* extended more than 3 mm below the surface. This results in an extremely high ratio of chlorenchyma surface area per unit stem surface area of 137. An analogous ratio for C_3 plants is about 15–30 (Nobel et al. 1975). Thus, a large surface area is available for CO_2 diffusion into the chlorophyll-containing cells of this cactus.

The optimal temperature for nocturnal stomatal opening of *Ferocactus cylindraceus* was about 12.6°C, which is quite similar to that recorded for other CAM plants

Fig. 3.17 Barrel cactus (*Ferocactus* cylindraceus), Arizona.

(Patten and Dinger 1969). That the stomata open preferentially on cool nights means less water loss, because the stem:air water vapour concentration differential tends to be lower than during warmer nights. Also, the biochemistry of CO_2 fixation by *Ferocactus cylindraceus* is also well adapted to cool nocturnal temperatures. This species naturally occurs in regions that have winter rains and that are cool at night for a large part of the year (Shreve and Wiggins 1964).

Ferocactus cylindraceus swells up on encountering rain, and shrinks when there is drought. This is accompanied by changes in internal solutes, with higher values recorded during drought (approximately twofold changes during drought). As might be expected of such a succulent CAM plant, it can use up to 33% of its mass for nocturnal stomatal opening without any major uptake of water from the soil and a further 17% during a sustained 4-month-long drought (Nobel 1977).

3.7.1.3 *Agave deserti (Agavaceae or Agavoideae)*

This monocot plant also has CAM. Similar to *Ferocactus cylindraceus*, it has a very shallow root system (mean root depth = 8 cm), which allows it to respond to brief pulses of rain (Noble 1976; Jordan and Nobel 1984). Succulent plants often have very shallow root systems (see also Von Willert et al. (1992) for examples from the Namib Desert) to exploit brief pulses of rain. For the summer, no stomatal opening occurs (and, hence, no photosynthesis) but it could be induced by watering (Hartsock and Nobel 1976). As was the case with *Ferocactus cylindraceus*, this species could also use water storage, so that stomatal opening could occur even when the water potential of the soil was less than plant water potential. Full stomatal opening occurred just 48 h after rain. As is the case with several other CAM species, optimal temperatures for photosynthesis occurred at about 15°C.

3.7.2 Leaf succulents

In leaf succulents, nearly the entire leaf is succulent (e.g. *Lithops, Aloe, Crassula*, and *Haworthia*). In many species, the stem is extremely short or even non-existent. In some species of *Crassula*, the stem is not succulent but the leaf is covered with a wax-like epidermis. Leaf succulents may include halophytic species of Chenopodiaceae, which have a strongly defined cuticle. In *Lithops* and *Conophytum* species, the leaf area is minimized and evaporative areas are small. Other species, such as those in the genera *Aloe* and *Haworthia*, form rosettes that minimize radiation from the sun and from the soil. In times of extreme drought, leaf succulents may also lose their leaves.

Turner and Picker (1993) examined two species in the genus *Lithops* (Mesembryanthema, Aizoaceae, common name 'stone plants'), which consists of leaf succulents that appear stone-like, submerged in the rocky surfaces that they live in. The only part of the plant that lies above the soil surface is about 0.5 cm, which has a window of variable opacity (Fig. 3.18) (Turner and Picker 1993). Many of the common mechanisms for controlling leaf temperatures (e.g. radiation with the surroundings, convective cooling, and evaporation) are not available for these plants because they are submerged in the soil. Turner and Picker (1993) ran a mathematical model using standard models of a plant and field measurements of populations near Ceres in the succulent Karoo (Western Cape, South Africa; mean annual rainfall = 400–500 mm) and on the Hamiltonberg near Walvis Bay, Namibia (< 100 mm mean annual rainfall), and showed that leaf temperatures are governed by the following: (1) leaf and soil temperatures are

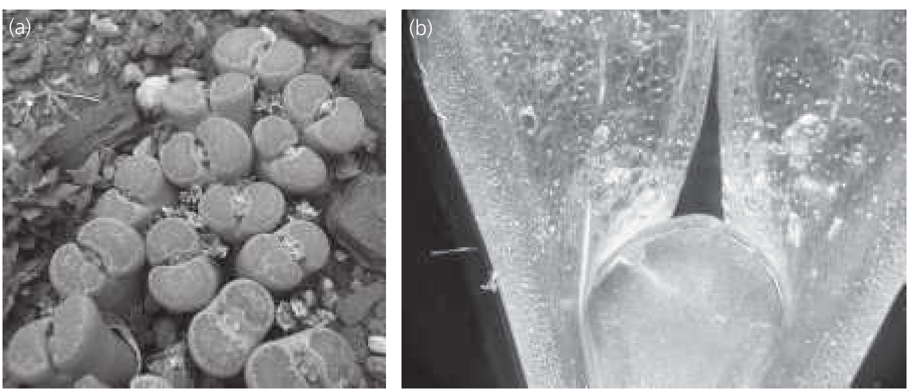

Fig. 3.18 The genus *Lithops* (Mesembryanthema, Aizoaceae, common name 'stone plants') consists of (a) leaf succulents that appear stone-like, submerged in the rocky surfaces that they live in. The only part of the plant that lies above the soil surface is about 0.5 cm, which (b) has a window of variable opacity.

Source: Photo of *Lithops salicola* (a) by Dysmorodrepanis under Creative Commons licence. Photo (b) by Yellowcloud under Creative Commons licence.

linked; (2) variations in surface energy budgets of the leaves have little effect on leaf temperature; and (3) variation in window clarity causes significant changes in leaf temperature. The effects of these are as follows: (1) thermally coupling the plant and soil combines the plant's thermal capacity with the soil's thermal capacity and reduces daily variation in leaf temperature; (2) the steep vertical variation in temperature that occurs in soils keeps the deeper parts of the plant cool relative to the hotter surface regions; (3) variation in leaf temperature is not related to variation in leaf colour (the leaves are cryptically coloured); and (4) variation in window clarity is probably the only thermal adaptation to hot conditions that embedded dwarf succulents employ.

3.8 Halophytes

Halophytes are plants that adapt in various ways to high salt regimes (Waisel 1972). The accumulation of saline and alkali salts in desert environments is due to high evaporation rates which exceed precipitation to the point that moisture in the soil is carried up to the soil surface, rather than leaching downwards (Day and Ludeke 1993). The salts are carried upwards with the rising moisture. Soil water in arid soils may contain between 2,000 and 20,000 ppm of salts (Fuller 1975).

There are two main types of halophytes (Waisel 1972):

1. Salt *accumulators* (usually NaCl) in vacuoles or specific organs, usually associated with succulence (e.g. Chenopodiaceae: *Salicornia, Suaeda, Chenopodium, Atriplex*). *Atriplex halimus* (Chenopodiaceae) is a large shrub (reaching up to 3 m) (Fig. 3.19). These shrubs are covered with vesiculated hairs, containing high concentrations of NaCl and oxalate. Under normal conditions, there is a positive

Fig. 3.19 Salt bush, *Atriplex halimus*, in the Negev Desert, Israel.

response to the addition of NaCl and no inhibitory effect on growth up to 100 mM was observed (Waisel 1972). Kam and Degen (1989) have shown that the rodent *Psammomys obesus* (Gerbillidae) can remove the saline surface of the *Atriplex* leaf and consume the leaves. This is sufficient to maintain the animal, even in lactation.

Phragmites australis (Poaceae) occurs as halophytic and glycophytic (non-salt tolerant) forms and can germinate in a wide range of saline media (0–0.5 M NaCl). High germination percentages (> 90%) were obtained in media with 0.4 M NaCl and slightly lower in 0.5 M NaCl. However, for the glycophytic ecotype, only 20% germinated at 0.4 M and 0% in the 0.5 M media (Waisel 1972).

Sarcobatus vermiculatus is a common halophyte north of 37°N in the Great Basin Desert in places such as Mono Lake and Owens Lake. It is spinescent with succulent, winter-deciduous leaves, although in warmer areas such as in the Mojave Desert, it may be evergreen (Danin 1996). Plants under water stress become more spiny. It may establish itself on habitats rich in salt. The sand of the *Sarcobatus* nebkas (phytogenic dunes) has a lighter colour than the surrounding ground (Danin 1996), probably because salts have been accumulated by recycling of salt-rich leaves deposited on the soil surface (Fireman and Hayward 1952). This species will not establish itself in non-saline soils in the presence of non-halophytic competitors.

2. Salt *excretors* (e.g. *Tamarix* and *Reaumuria* (Tamaricaceae)). *Tamarix aphylla* has growth that is inhibited by salinity at concentrations as low as 0.1 M NaCl but stops growing in a medium containing about 0.5 M NaCl (Waisel 1972). Ma et al. (2007) examined the stable carbon isotope ratios of the desert plant *Reaumuria soongorica* and the physicochemical properties of soil in the Gobi Desert. Specifically, they examined the correlations between δ^{13} C values and the soil factors in the major distribution areas in northwestern China. They found correlations between δ^{13} C values in *Reaumuria soongorica* that significantly increased with decreasing soil water content (SWC) and increasing total dissolved solids (TDS) in soil. There were no significant correlations between the δ^{13} C values and pH, total nitrogen, soil organic matter (SOM), total phosphorus, and effective phosphorus in soil. Ma et al. (2007) concluded that the variation in δ^{13} C values of *Reaumuria soongorica* was probably caused by stomatal limitation rather than by nutrient-related changes in photosynthetic efficiency.

Desert halophytes tend to rely on the accumulation of inorganic cations (mostly Na^+ and K^+) for osmotic adjustment to drought and salinity (Flowers et al. 1977; Flowers and Yeo 1986; Smith et al. 1997). *Drought tolerance* relies heavily on K^+ uptake and accumulation for osmotic adjustment, and *salinity tolerance* relies on Na^+ for osmotic adjustment. As a result, high sodium phenotypes (e.g. Chenopodiaceae) and low sodium phenotypes (e.g. Poaceae) (Flowers and Yeo 1986), or even subspecies of *Atriplex canescens* (Glenn et al. 1992), can be distinguished from one another on the basis of the evolution of ion accumulation in response to either drought stress or salinity.

3.9 Phreatophytes

A phreatophyte is a deep-rooted plant that obtains its water from the water table or from another deepwater source such as an aquifer. Some plants are obligate phreatophytes in that there is a strong positive association with the water table while in others the relationship is facultative. In *Acacia raddiana*, roots may be shallow to capture rain from floodwater in ephemeral rivers (wadis) and they have deep roots to maximize uptake from aquifers (Sher et al. 2010). Similar situations exist for *Tarchonanthus camphoratus* (Fig. 3.20) and *Acacia mellifera* (Fig. 3.21) in southern

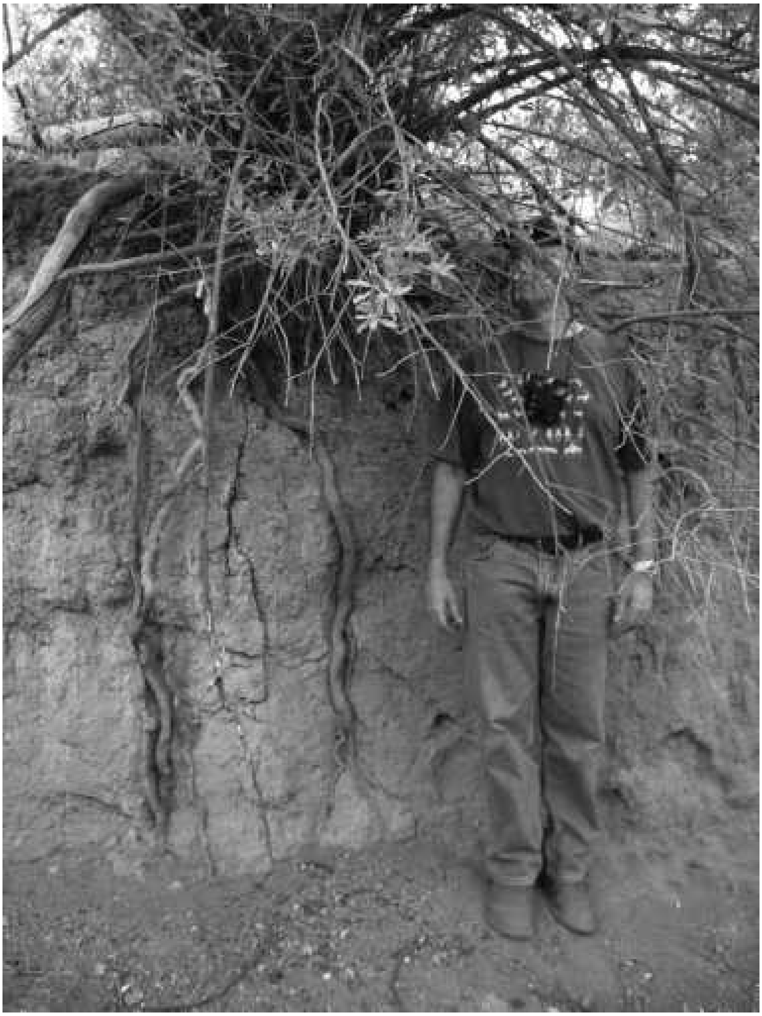

Fig. 3.20 Deep root of a *Tarchonanthus camphoratus* in the Northern Cape, South Africa.

Fig. 3.21 Shallow surface roots of *Acacia mellifera* in the arid Northern Cape, South Africa. These shrubs put down a long tap root to access groundwater and then send out lateral roots.

Africa (Kambatuku et al. 2013a). I note that, where *Tarchonanthus camphoratus* and *Acacia mellifera* occur together, Schleicher et al. (2011a) have shown that *Acacia mellifera* outcompetes the former species.

The mean maximum rooting depth worldwide was 4.6 ± 0.5 m, and the individual maximum rooting depth was 68 m for *Acacia erioloba* and *Boscia albitrunca*, the roots of which were found during well drilling in deep sandy soils in the central Kalahari Desert in Botswana (Jennings 1974). The 10 deepest rooting species are, in decreasing order, as follows: *Boscia albitrunca* (68 m), *Acacia erioloba* (60 m), *Prosopis juliflora* (53 m), *Eucalyptus marginata* (40 m), *Retama raetam* (20 m), *Tamarix aphylla* (20 m), *Andira humilis* (18 m), *Alhagi maurorum* (now *Alhagi graecorum*) (15 m), *Prosopis farcta* (15 m), and *Prosopis glandulosa* (15 m). Unsurprisingly, all but two of these species (*Eucalyptus marginata* and *Andira humilis*) are desert dwellers. Two additional plant species, *Populus euphratica* and *Tamarix ramosissima* from the Taklamakan Desert, have roots that are 22.7 and 23.7 m from groundwater. However, this is not because they grew down but rather because the dunes have grown up around the stem of the trees (Gries et al. 2003).

3.9.1 Hydraulic lift

Hydraulic lift occurs when water is lifted by the roots from moist areas to drier areas of soil (Richards and Caldwell 1987). The first field evidence of hydraulic lift was

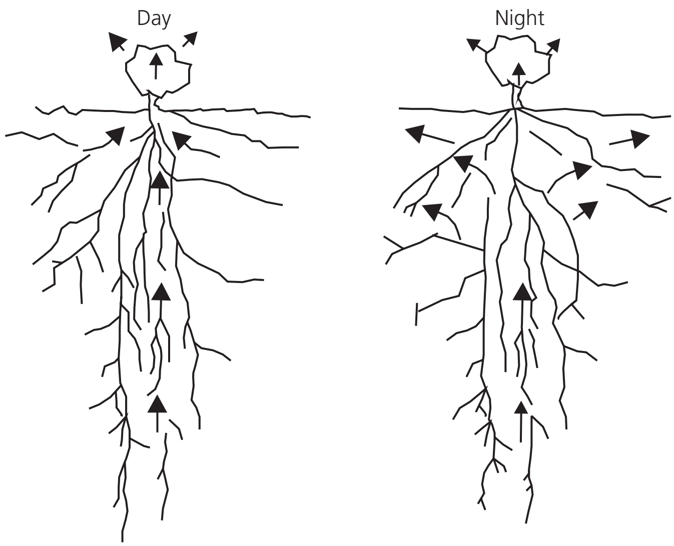

Fig. 3.22 Pattern of water flow through the root system during day and night periods according to the hydraulic lift hypothesis. (a) During the day, water is absorbed from all depths in which soil moisture is available and passes into the transpiration stream. (b) At night, when transpiration is reduced and plant water potential rises, the primary pathway for water movement is from moist soil through the root system to drier soil layers.

Source: Modified from Caldwell et al. (1998). With kind permission of Springer.

shown in the desert shrub *Artemisia tridentata*. When the shrubs were covered with opaque plastic bags, water potential rose continuously for more than 2 days until the shrubs were again exposed to daylight. When the shrubs were illuminated at night, the increase of water potential was suppressed (Richards and Caldwell 1987). Water that is released from the roots when transpiration ends (usually at night) usually passes into the upper soil layers where it is absorbed and then re-absorbed by the plant the following day and then transpired. Part of the process involves reverse flow, where the water passes by osmosis out of the xylem of the upper roots (when transpiration ceases) into the dry neighbouring soil (Fig. 3.22). Hydraulic lift has been shown in many trees and shrubs, mostly in arid and semi-arid regions (23 species of grasses, herbs, shrubs, and trees). Using isotopes of deuterium, Richards and Caldwell (1987) showed that water taken up by the roots of *Artemisia tridentata* was subsequently detected in the adjacent roots of grass plants. In this species, up to 33% of the daily evapotranspiration may be returned to the upper soil layers. A number of different plant species may benefit from hydraulic lift (Fig. 3.23; e.g. *Acacia erioloba* benefitting *Tarchonanthus camphoratus*). Prieto et al. (2010) conducted transpiration suppression experiments during spring 2005 in Chile and spring 2008 in arid parts of Spain on five shrub species that employed hydraulic lift, viz. *Flourensia thurifera, Senna cumingii*, and *Pleocarpus revolutus* (Chile), and *Retama sphaerocarpa* and *Artemisia barrelieri* (arid

Fig. 3.23 Facilitation of a number of plant species under the canopy of *Acacia erioloba* in the arid Northern Cape province (South Africa) probably occurs as a result of hydraulic lift and, perhaps, increased nitrogen levels because *Acacia erioloba* is known to fix nitrogen.

Spain). Shrubs were covered with a black, opaque plastic fabric for a period of 48–72 h, and soil water potential was recorded at different depths under the shrubs. While the shrubs remained covered, water potential continuously increased in shallow soil layers until the cover was removed. They found that the amount of water lifted by shrubs is heavily dependent on soil texture; shrubs that grew in loam soils redistributed up to 3.5 times more water than shrubs growing on sandy soils (Prieto et al. 2010).

Cardon et al. (2013) found that hydraulic lift may also increase the amount of nitrogen cycling. Cardon et al. (2013) explored the role of hydraulic lift in sagebrush *Artemisia tridentata* by augmenting deep soil water availability to plants throughout a summer growing season. The water-augmented sagebrush lifted greater amounts of water than control plants and was slightly less water stressed (less negative predawn and midday leaf water potentials). Soil respiration also increased under water-augmented plants. At the end of the summer, application of a ^{15}N isotopic labelling technique revealed increased rates of nitrogen cycling in surface soil layers around water-augmented plants. Also, there was increased uptake of nitrogen into the inflorescences of water-augmented plants when *Artemisia tridentata* set seed.

Kambatuku et al. (2013a) tested Walter's (1939) two-layer hypothesis, which predicts that trees have deeper roots than grasses and are capable of taking water from groundwater and/or aquifers that grasses do not have access to. In open savannas, grasses tend to outcompete trees (Grellier et al. 2012; Ward et al. 2013; Tjelele et al. 2015) because they are able to access water from rainfall. When there is heavy grazing, grasses are removed and, consequently, trees are capable of encroaching en masse. Kambatuku et al. (2013a) conducted a greenhouse experiment on *Acacia mellifera*, a common encroaching species in the arid savannas of the Northern Cape (and Namibia). This species encroaches on both rocky and sandy soils, although it tends to reach higher densities on rocky soils (Britz and Ward 2007). Kambatuku et al. (2013a) set out to determine whether tree seedlings and grasses obtained water from different depths on rocky and sandy soils and the influence of repeated grass clipping on soil moisture. They used 60-cm-deep bins for the experiment. Grass competition significantly reduced tree seedling rooting depth on both rocky and sandy substrates, as predicted by Walter's (1939) two-layer hypothesis. Trees had significantly longer roots on rocky substrates than on sandy substrates for all combinations (trees only, trees with unclipped grasses, and trees with clipped grasses). Their results indicated a three-tier soil moisture depletion pattern, with a top layer (15 cm) exclusively exploited by grasses, an intermediate zone (25–35 cm) exploited by both grass and tree seedling roots, and deeper subsoil exclusively exploited by tree seedling roots (Fig. 3.24). Their results are consistent with Walter's two-layer

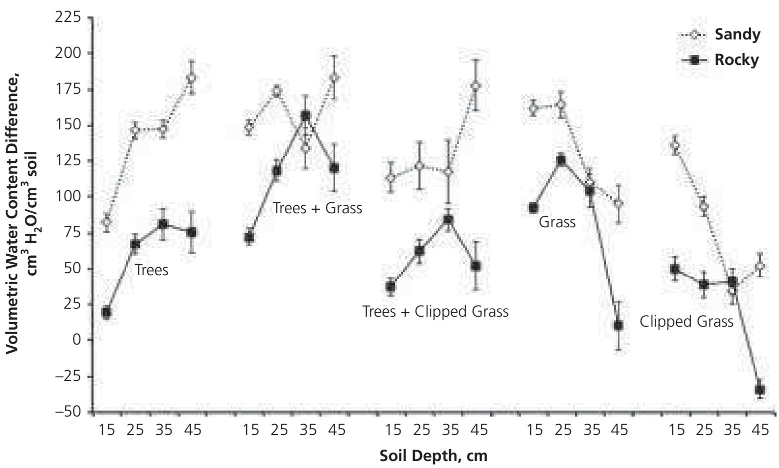

Fig. 3.24 The differences in mean ± standard error (S.E.) volumetric soil water content of complete controls (no vegetation) and vegetated treatments on sandy and rocky substrates for *Acacia mellifera* and grasses with increasing depth. Clipped grass means that the grass was clipped to simulate herbivory.

Source: From Kambatuku et al. (2013a). With kind permission of John Wiley.

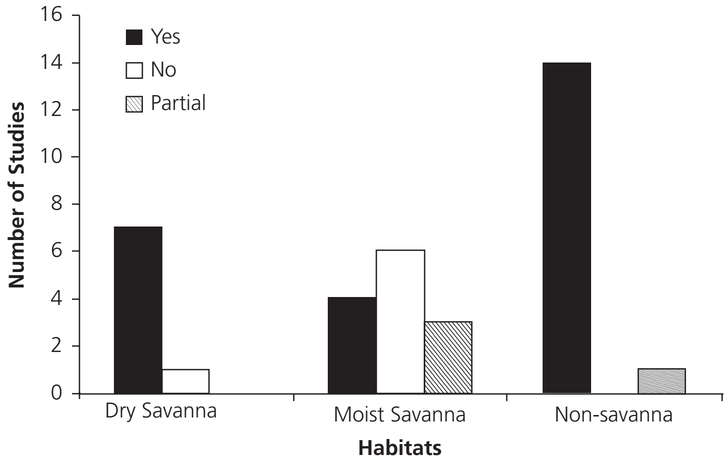

Fig. 3.25 Support for Walter's (1939) two-layer hypothesis. Yes = the study supported Walter's hypothesis, No = Walter's hypothesis was not supported, and Partial = one shrub or tree species had deeper roots than grasses and one did not.

Source: From Ward et al. (2013). With kind permission of Springer.

hypothesis, but they distinguished three rather than two layers of tree and grass root interactions in acquiring soil moisture. These results are consistent with those of Ward and Esler (2011), who showed in a field experiment that grazing (of grasses) resulted in a significant increase in *Acacia mellifera* recruitment and survival regardless of substrate type (sand or rock).

A global review of Walter's two-layer hypothesis was performed by Ward et al. (2013). They differentiated between dry savannas (< 650 mm mean annual precipitation (MAP)), moist savannas (> 650 mm MAP), and non-savannas. All but two of the non-savannas were in deserts (Fig. 3.25). They found that most studies of root depth in dry savannas supported Walter's (1939) two-layer hypothesis, as did most non-savanna studies. However, the support in moist savannas was much more mixed and slightly more studies in moist savannas did not support Walter's (1939) hypothesis. Walter's (1939) hypothesis was originally established in Namibia, where it is clear that there are distinct benefits to tree roots being able to access groundwater, especially when competing with grasses.

It is also possible for the reverse process, known as inverse hydraulic lift, to occur. Inverse hydraulic lift occurs when roots move water down into the deeper soils and allow the water to flow into the dry sand there (Schulze et al. 1998). It is claimed that this may allow roots to grow easily in dry soil so that the roots can get down into these deep soils (Schulze et al. 1998). For this reason, the term 'hydraulic lift' is more commonly known as 'hydraulic redistribution' to recognize that water can be redistributed by roots in various directions from wet to dry soils (Katul and Siqueira 2010; Domec et al. 2012; Hao et al. 2013).

4 Morphological, Physiological, and Behavioural Adaptations of Desert Animals to the Abiotic Environment

Animals must be able to withstand the lack of water and the high and low temperatures in deserts to survive there. Many animals show unique morphological adaptations to desert extremes, while others are able to avoid these by behavioural means. This chapter will focus on patterns of convergent evolution of traits to assess which features represent unique desert adaptations.

Willmer et al. (2000) consider there to be two major strategies to deal with extremes of temperature: evaders and endurers. As the names imply, evaders avoid the heat such as by using burrows and endurers tolerate it. According to Willmer et al. (2000), a third group inhabits warm desert habitats, namely, evaporators. The latter group uses evaporative cooling to endure the heat. Roughly speaking, small organisms (<20 g) are evaders, intermediate-sized organisms are evaporators, and large organisms (mostly mammals and very large birds) are endurers. The main reason that these categories are linked in this way is that there is a simple relationship between surface area and volume. A small organism, if it had cubic dimensions, may have a surface area of, say, 1 cm × 1 cm × 6 sides = 6 cm^2. Its volume will be 1 cm × 1 cm × 1 cm = 1 cm^3. A slightly larger organism will be, say, 2 cm × 2 cm × 6 sides = 24 cm^2. Its volume will be 2 cm × 2 cm × 2 cm = 8 cm^3. An even larger organism may be 3 cm × 3 cm × 6 sides = 54 cm^2. Its volume will be 3 cm × 3 cm × 3 cm = 27 cm^3. Thus, the small organism will have a surface area:volume ratio of 6:1, an intermediate-sized organism will have a ratio of 24:8 = 3:1, and a large organism will have a ratio of 54:27 = 2:1. This means that a small organism will be able to gain heat and lose it again quite quickly through its large surface area, whereas a large organism will find it considerably more difficult to do so.

Small organisms tend to be convectively coupled, meaning that wind affects their body temperatures greatly because of their relatively large surface areas. On the other hand, large organisms tend to be radiation coupled (heat, either directly from the sun or reflected from the ground (albedo), affects their body temperatures greatly because of their relatively small surface areas (Pianka 2011)). Furthermore, most invertebrates, amphibians, and reptiles are ectothermic because they have external heat sources only and, consequently, the body temperature they have is affected by

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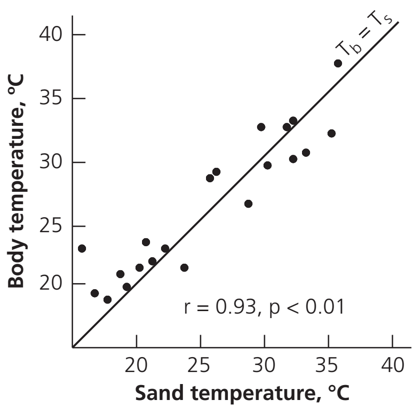

Fig. 4.1 Body temperature (T_b) fluctuations closely match those of sand temperature (T_s) fluctuations in the Namib golden mole.

Source: From Fielden et al. (1990). With kind permission of Elsevier.

the convection and radiation around them. Conversely, birds and mammals are considered endothermic because they have an internal heat source and, consequently, their body temperatures are less variable. Another set of terms for these are heterotherms (also known as *poikilotherms*) and homeotherms (also known as *homoiotherms*), respectively. However, some animals do not fit into this generalization very well. For example, the Namib Desert golden mole, *Eremitalpa granti namibensis* (Chrysochloridae; Insectivora), is a 15- to 40-g mammal yet allows T_b to fluctuate considerably while under the soft dune sand where it lives (Seymour et al. 1998) (Fig. 4.1). The physiology of the sand-swimming marsupial mole *Notoryctes caurinus*

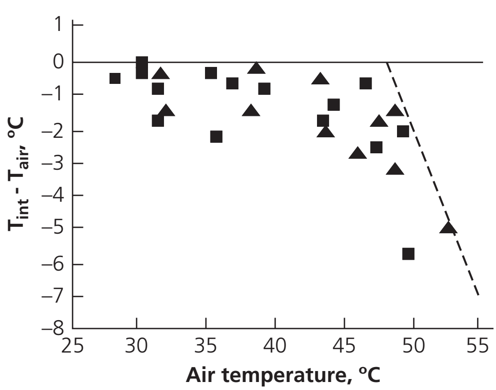

Fig. 4.2 Depression of internal temperature relative to air temperature in grasshoppers, *Poekilocerus bufonius*. Female grasshoppers could maintain relatively constant body temperatures up to an air temperature of about 48°C.

Source: From Prange and Pinshow (1994). With kind permission of Elsevier.

from Australia is convergent with the Namib Desert golden mole *Eremitalpa granti* and may display similar patterns of change in T_b (a value of 30.8°C has been recorded for this species). However, more data are needed on this marsupial mole before anything convincing can be said about body temperature fluctuations (Lovegrove 2012). In a counterexample of body temperature control, in the Negev Desert, Prange and Pinshow (1994) showed that female 5.5-g grasshoppers, *Poekilocerus bufonius*, could maintain relatively constant body temperatures up to an air temperature of about 48°C (Fig. 4.2) by evaporative cooling. Desert cicadas (Toolson 1987; Sanborn et al. 1990) and large beetles (Bartholomew and Casey 1977) are also endothermic insects. Nonetheless, in general, evader, evaporator, and endurer are useful categories, although there is a lot of overlap between the categories of evaders and evaporators and they will be condensed into a single category here.

4.1 Evaders and evaporators

Small animals, generally classified as evaders, include invertebrates (with the notable exceptions listed earlier), desert amphibians and reptiles, and also smaller mammals, rodents, and insectivores. The term 'evader' refers to the animal's behaviour, which helps to prevent overheating of the body on hot sunny days (Plate 15) and avoids the need for cooling by evaporative water loss, which is not feasible for small animals living in an arid habitat. Evaders make use of microenvironments such as shady rock crevices, underground burrows (Fig. 4.3), and shade cast by plants for behavioural thermoregulation. Evaders also use behaviour to prevent excessive cooling of the body, retreating to shelter when T_a declines at night. Willmer et al. (2000) define

Fig. 4.3 Cast of a burrow of a scorpion, *Scorpio palmatus*, in the Negev Desert.
Source: Photo by Berry Pinshow.

evaporators as animals that depend on sufficient water intake to enable them to cool T_b by evaporation. Few of these species can survive in deserts, and those that do either live on the edges of deserts where they can access water or have behavioural and physiological adaptations that reduce reliance on evaporative cooling. So for evaporators, evasion may be an important part of their thermoregulatory strategy. Evaporators include medium-sized mammals such as jackrabbits, dogs, foxes, and also desert birds such as larks. There is a lot of overlap here in the evaporator classification for both evaders and endurers, so one must be aware that some species could fit into either. For example, both evaders and endurers will cool themselves evaporatively.

Insects possess some of the most effective desert features. For example, they have a very small body size, which means that they have a large surface area:volume ratio, and, consequently, they can offload heat quickly and gain it quickly when the day is cool. Many species, particularly tenebrionid beetles, have a waxy cuticle to reduce water loss across the body surface. The most extreme form of this is the wax bloom in Namib Desert and North American tenebrionid beetles (Hadley 1979; McClain et al. 1985) (Fig. 4.4). Another important feature is a discontinuous ventilation cycle. Insects and solifugids (Solifugidae: Arachnidae; also known as sun or wind spiders) use this system (Lighton and Fielden 1996), as do ixodid ticks (family Acari) (Fielden et al. 1993). However, the 'sit-and-wait' strategy employed by ticks, where they are inactive for long periods while waiting for a blood meal, might predispose them to a discontinuous ventilation strategy (Fielden et al. 1993). Spiracles are kept closed for >10 min to minimize respiratory water loss (Lighton and Fielden 1996). Spiracles must then be opened for gas exchange. This is an effective way of limiting

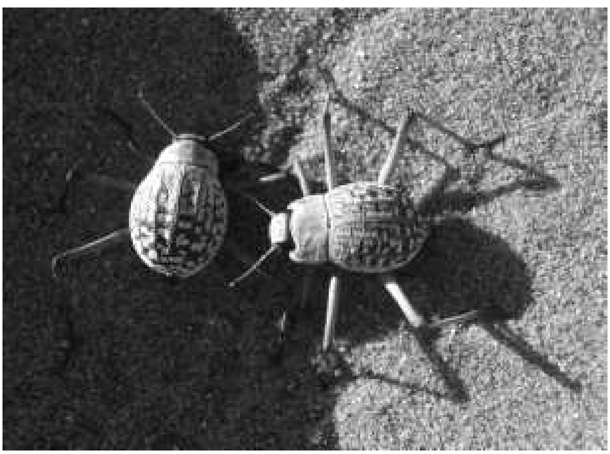

Fig. 4.4 Wax blooms in *Onymacris rugatipennis*, Namib Desert tenebrionid beetles. Lighter areas on the beetles indicate wax bloom.

Source: Photo by Thomas Schoch under Creative Commons licence.

water loss. In solifugids, there are three phases similar to those in insects comprising (1) a closed-spiracle phase, followed by (2) a diffusive phase characterized by tissue-level O_2 uptake but very low CO_2 emission (functionally equivalent to the insect fluttering-spiracle phase), and, finally, (3) an open-spiracle phase during which accumulated CO_2 escapes. In solifugids, in the open-spiracle phase CO_2 emission volume was independent of temperature and metabolic rate, comprising 20 μL g^{-1} body mass (Lighton and Fielden 1996).

Insects, land snails, and many reptiles and birds excrete uric acid as a major nitrogenous waste while mammals excrete urea. Uric acid is largely insoluble in water and is excreted as paste, resulting in very little water loss. Most excretory systems (regardless of whether they are invertebrates or vertebrates, exotherms or endotherms) produce urine by refining a filtrate derived from body fluids. These systems are generally developed from a system of complex tubules. In the case of insects and other terrestrial arthropods, they use Malpighian tubules to excrete nitrogenous wastes and function in osmoregulation. Phillips (1964) has shown that insects such as the desert locust, *Schistocerca gregaria*, produce a relatively dry waste that is important for desert life to avoid excessive water loss. He showed that the maximum osmotic gradient of locusts fed a hypertonic saline solution was 2–3 times higher than locusts fed tap water, indicating considerable ability to regulate water absorption in relation to their requirements (Fig. 4.5). They are able to produce a reusable rectal fluid that is about 20 μL as opposed to locusts fed tap water that do not produce any reusable fluid. Mammals from very dry environments such as the South American red vizcacha rat, *Tympanoctomys barrerae* (Ojeda et al. 1999), have very long loops of Henle to concentrate the ions and remove water for reuse (Fig. 4.6). They also use countercurrent multipliers within the loops of Henle to effectively concentrate their nitrogenous wastes (Fig. 4.7).

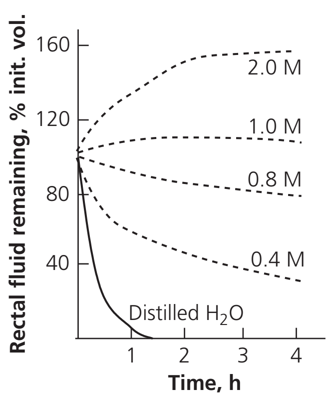

Fig. 4.5 Phillips (1964) showed that the maximum osmotic gradient of locusts fed a hypertonic saline solution was 2–3 times higher than locusts fed tap water, indicating considerable ability to regulate water absorption in relation to their requirements.

Source: From Phillips (1964). With the kind permission of Oxford University Press.

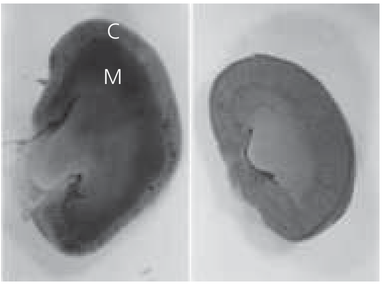

Fig. 4.6 Longitudinal sections of kidneys from *Tympanoctomys* and its close relative *Octomys.* Note the difference in the thickness of the cortex (C) and medulla (M) area. The medulla contains the loops of Henle, which extract salts and water. *Tympanoctomys* feeds on saltbush (hence, the thick medulla and long renal papilla), whereas *Octomys* feeds on cacti (and other plants) and does not need a specialized kidney like that of *Tympanoctomys*.

Source: Photograph courtesy of Ricardo Ojeda.

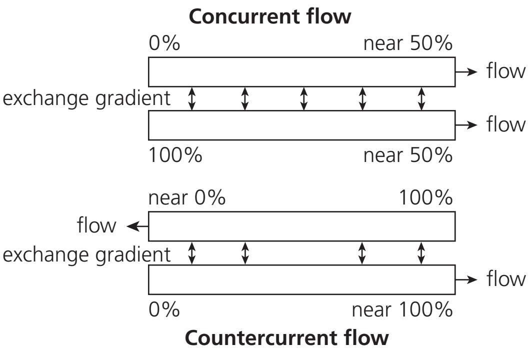

Fig. 4.7 Countercurrent multipliers within the loops of Henle effectively remove water from urine so that the body can retain water used to move the nitrogenous waste products. The diagram presents a generic representation of a concurrent and a countercurrent exchange system, with tubes containing fluid separated by a semipermeable membrane. Fluid is transferred across the barrier in the direction from greater to lesser according to the second law of thermodynamics. In the concurrent exchange system, the liquid flows in the same direction. A concurrent exchange system has a variable gradient over the length of the exchanger. With equal flows in the two vessels, this exchange method is capable of moving half of the property from one flow to the other, no matter how long the exchanger is. However, with the two flows moving in opposite directions, the countercurrent exchange system can maintain a nearly constant gradient between the two flows over their entire length.

4.1.1 Snails

One might think that snails would be rare animals in deserts, especially in limestone deserts such as the Negev Desert of Israel. They occur, to varying degrees, in all deserts. They have unique adaptations for desert life. In the Negev Desert, these snails can be found in a dormant state on the barren soil surface fully exposed to the sun in summer. Although some species develop calcareous epiphragms to reduce water loss from their shell openings, some use a mucous covering (Ward and Slotow 1992; Arad 1993), while others climb to the tops of plants to aestivate (Fig. 4.8). In winter, they become active during rainy periods, when they feed and reproduce. In the southern Namib Desert, Dallas et al. (1991) examined water exchange, temperature tolerance, and oxygen consumption of the snail, *Trigonephrus* sp., and related this to activity. Body temperature tracked sand temperature. Snails tolerated sand temperatures as high as 45°C. Mean oxygen consumption rates were 32.0 μL O_2 g^{-1} total body $mass^{-1}$ h^{-1} at 15°C when the snails were active, and 11.27 μL O_2 g^{-1} total body $mass^{-1}$ h^{-1} at 25°C when the snails were inactive. These values are 2–6 times lower than those recorded for the similarly sized mesic snail, *Helix aspersa*. At 25°C and 15% relative humidity (RH), mean water loss was 5.95 mg day^{-1}. Activity experiments indicated that low ambient temperatures and high humidities were favoured by the snails. This, together with the burying behaviour of these snails during high temperatures, suggests that they limit stress by restricting activity to physiologically

Fig. 4.8 *Theba pisana snails* at the tops of fence poles at Kadina, South Australia

Source: Photo used by Creative Commons licence.

favourable periods, even though more extreme conditions may be tolerated. Shachak and Steinberger (1980) found that the preference of *Sphincterochila zonata* for low ambient temperatures and high humidities may restrict their activity to just 8–27 winter days annually (determined over 7 years of observations).

In the Negev Desert, Schmidt-Nielsen et al. (1971) found that lethal temperatures of *Sphincterochila boisseri* lie between 50 and 55°C, depending on the time of exposure. The temperature of the dormant animal within the shell, exposed to the sun on the soil surface in summer, does not reach a lethal level, although the temperature of the surrounding soil surface far exceeds this temperature. The oxygen consumption of dormant *Sphincterochila boisseri* snails varies with temperature (Q_{10} = 2–4) (Schmidt-Nielsen et al. 1971). It is so low that the tissues could support this metabolic rate for several years, thus permitting continued dormancy even during periods of drought extending over more than 1 year.

The rate of water loss from dormant *Sphincterochila boisseri*, exposed in their natural habitat in summer, is about 0–5 mg day^{-1} per snail (Schmidt-Nielsen et al. 1971). This rate, if continued unchanged, would give an annual loss <200 mg. A 4-g specimen contains about 1400 mg water, and because the water loss during the cooler part of the year is lower, several years should elapse before critical levels of water loss would be reached. In snails collected in summer, the water content was not reduced, indicating no measurable depletion of water reserves during the hot season. However, Arad et al. (1990, 1993) showed that other Negev Desert snails such as *Sphincterochila zonata*, lost 4% of their body mass over 3 weeks, while mass loss for *Trochoidea simulata* was 5–7%. In another study, Arad (1993) found that *Eremina desertorum* lost 0.31% day^{-1}, *Euchondrus desertorum* lost 0.42% day^{-1} (= 9% mass loss over 21 days), and *Euchondrus albulus* lost 0.63% day^{-1} as adults (= 13.2% over 21 days) and almost double that (1.04% day^{-1}) as juveniles. Arad (1993) ascribes the higher values to the more mesic distribution of this last-mentioned species. The mean body mass of *Eremina desertorum* was 3.3 g, and for *Euchondrus desertorum* was 0.19 g and for *Euchondrus albulus* was 0.07 g. The small size of the last two species allows them to hide under rocks for most of the day and emerge at night (Fig. 4.9). They do not need to close off the shell entrances to moisture because the entrance to the shell is very contorted.

Arad et al. (2010) tested whether adaptation to different habitats in the field affects the endogenous levels of heat shock proteins (HSPs) in two closely related *Sphincterochila* snail species from Israel. One of these species was a desiccation-resistant desert species, *Sphincterochila zonata*, and a Mediterranean-type, desiccation-sensitive species, *Sphincterochila cariosa*. They examined HSP levels in various tissues of snails during aestivation and after resumption of activity. Aestivation is a form of dormancy, which is a metabolic depression also known as hypometabolism because the animals minimize their metabolic rates to reduce energy output. Aestivation enables animals to survive lack of water and high T_a during a hot, dry season. During aestivation, the Mediterranean species, *Sphincterochila cariosa*, had higher standing stocks of HSP70 in the foot and the hepatopancreas, and of small HSPs (sHSPs) in all the examined tissues, whereas the desert species, *Sphincterochila zonata*, had higher stocks of HSP70

Fig. 4.9 *Eremina desertorum* snails are about 10–12 mm long, yet they play an important role in the cycling of nitrogen in the Negev Desert ecosystem.

Source: From http://www.cpbr.gov.au/cryptogams/underworld/panel-12/index.html. Date accessed: 22 February 2016.

in the kidney and of HSP90 in the kidney and in the hepatopancreas. Arousal from a hypometabolic state (aestivation) induced a general upregulation of most HSPs. However, the expression of HSP90 in the foot in both species was higher during aestivation. These authors suggest that the stress protein machinery is upregulated during arousal in anticipation of possible oxidative stress ensuing from the accelerating metabolic rate and subsequent exit from aestivation. These findings indicate that aestivation and activity represent two distinct physiological states. They suggest that land snails use HSPs as important components of the aestivation mechanism, and as part of their survival strategy during and after arousal.

4.1.2 Frogs

The ultimate vertebrate evaders are desert frogs such as *Cyclorana platycephala* (Fig. 4.10), *Limnodynastes spenceri* and *Neobatrachus pictus* from Australia, which spend most of the year in aestivation, inside a burrow (Lee and Mercer 1967). The North American Desert spadefoot toad, *Spea couchii*, also aestivates (Mayhew 1965). Lee and Mercer (1967) found that the cocoon that envelopes the Australian frog, *Neobatrachus pictus*, is identical to the stratum corneum of the epidermis and is derived by sloughing this layer as a single unit (see also Mayhew (1965) for *Spea couchii*), as occurs in snakes. During the short rainy season, desert frogs accumulate water in the bladder, where it remains during aestivation. Thereafter, the frogs use the accumulated water to osmoregulate.

Green-striped burrowing frogs, *Cyclorana alboguttata*, from Australia survive droughts by entering aestivation, characterized by a reduction in resting oxygen consumption by as much as 80% (Hudson et al. 2008). Aestivation in *Cyclorana alboguttata* is manifest by transcriptional silencing of skeletal muscle bioenergetic genes at

Fig. 4.10 Australian desert frog, *Cyclorana platycephala.* During aestivation, the frogs are protected from losing water to the dry soil in the burrow by a cocoon. At the end of the rainy season, the frogs burrow into the soil, and the skin undergoes a type of moulting process in which layers of epidermis are separated from the body but not shed, forming a protective cocoon, covering all parts of the body apart from the nostril openings. The cocoon thickens, becoming heavily keratinized, and prevents loss of water from the frog's body during the 9–10 months of aestivation.

Source: Photo from M. Robinson (1999) licensed to OpenLearn under a Creative Commons Licence.

the time of aestivation. These authors assessed mRNA transcript abundance of seven genes that code for proteins with established roles in epigenetically mediated gene silencing. They found coordinated upregulation of these genes in 6-month-old aestivating muscle of these frogs, particularly in transcriptional co-repressor SIN3A and DNA (cytosine-5-) methyltransferase 1. These data indicate that the transcriptional silencing of skeletal muscle genes and metabolic depression that occurs during seasonal dormancy are ways that this desert frog shuts down its metabolism to remain dormant for long periods.

4.1.3 Rodents

Some of the most well-known organisms in deserts are granivorous rodents. In their own ways, they too are evaders. Kangaroo rats and jerboas (Plate 16), for example, appear to be ill-adapted for life in a desert because, similar to other rodents, they neither sweat nor pant. Nevertheless, inside the burrow, they could lose water by evaporation from the lungs, which would be enhanced by T_b being higher than burrow T_a. As the water-carrying capacity of air increases with temperature, warm expired air contains more water than the cooler inhaled air (see the discussion about *Meriones crassus* in the next paragraph). However, the temperature of the exhaled air in kangaroo rats is lower than that of T_b, and often close to T_a (Fig. 4.11). This is

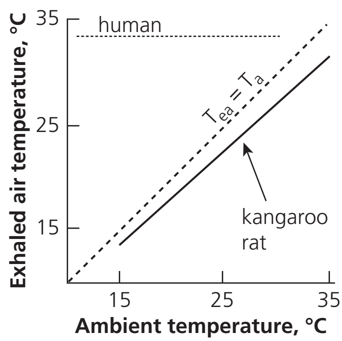

Fig. 4.11 Kangaroo rats *Dipodomys* spp. depend on metabolic water because there is virtually no water available in their diet of seeds. Inside the burrow, they could lose water by evaporation from the lungs, which would be enhanced by T_b being higher than burrow T_a. As the water-carrying capacity of air increases with temperature, warm expired air contains more water than the cooler inhaled air. However, the temperature of the exhaled air in kangaroo rats (T_{ea}) is lower than that of T_b, and often close to T_a, because the nasal passages (turbinates) of kangaroo rats are extremely narrow and convoluted and provide a temporal countercurrent cooling system, which operates as a heat exchanger.

Source: This modified figure is licensed to OpenLearn under a Creative Commons Licence.

because the nasal passages (turbinates) of kangaroo rats are extremely narrow and convoluted and provide a temporal countercurrent cooling system, which operates as a heat exchanger (MacMillen 1972).

Shenbrot et al. (2002) have shown that jirds, *Meriones crassus* (Gerbillidae, Rodentia; body mass range = 50–110 g, mean for non-lactating females = 80 g), have remarkably stable burrow temperatures. Although there are large differences between seasons (14°C in winter and 31°C in summer in sand and about 10°C in winter and 28°C in summer in loess), there is almost no variability in these temperatures (Fig. 4.12). Similarly, relative humidity is remarkably constant. Thus, although mean air temperatures may be lower than burrow temperatures, it is the escape from high air temperatures in the middle of the day, especially in summer, that make the burrow such a suitable place to rest. Conversely, the red vizcacha rat, *Tympanoctomys barrerae* (Octodontidae, Rodentia), of the Monte Desert in Argentina has non-random orientation of its burrow openings to face away from the cold winds in winter and into direct sunlight (Torres et al. 2003). It is apparent that burrows are very effective places to avoid either heat or cold. An additional issue is high CO_2 build-up in rodent burrows (Ganot et al. 2012; Brickner-Braun et al. 2014; Turner and Pinshow 2015). Ganot et al. (2012) have found that thermal convective venting in an inclined burrow could ventilate burrows at two orders of magnitude more than the calculated levels of CO_2 production by *Meriones crassus*, even without potential venting mechanisms such as diffusion through the soil and wind-driven venting. Brickner-Braun et al. (2014) showed that, even at low wind speeds, the random penetration of eddies into

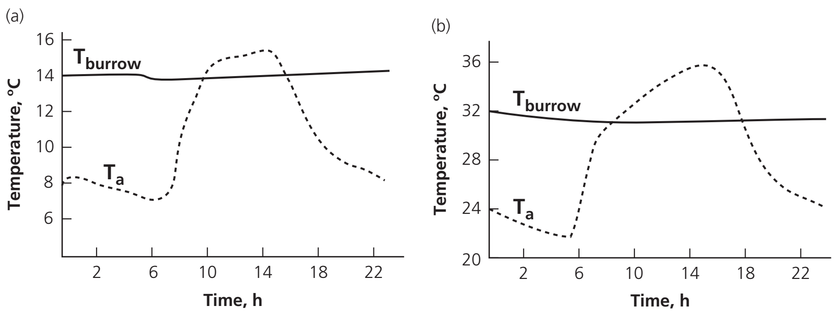

Fig. 4.12 There was no variability in burrow temperatures of *Meriones crassus* in (a) winter and (b) summer, indicating the stability of sand temperatures. Note that burrow temperatures differ considerably between winter and summer.

Source: From Shenbrot et al. (2002). With kind permission of Elsevier.

a burrow through its openings is sufficient to keep the burrow CO_2 low enough to be physiologically inconsequential (see also Turner and Pinshow 2015).

One of the unique morphological characteristics of an evader/evaporator is the bushy tail of the Cape ground squirrel, *Xerus inauris*, which lives in the Kalahari, Karoo and Namib deserts of southern Africa. This tail acts as a parasol (umbrella), reducing the high body temperatures of these small mammals (Bennett et al. 1984). By using taxidermic models covered with the pelt of the animal, Bennett et al. (1984) measured the operative environmental temperatures (T_e) of models with raised tails (Fig. 4.13) and in a prone position. T_e is an effective way of measuring the integrated radiant and convective thermal heat of an organism, and is the equilibrium

Fig. 4.13 *Xerus inauris* shading itself with its unique bushy tail.

Source: Photograph used by Creative Commons licence.

temperature the organism would attain if it lacked metabolic heat and evaporative water loss (Bakken 1980). Between 09h15 and 11h30, squirrels usually raised their tails and faced their backs to the sun. After 11h30, most squirrels started disappearing from the surface, shuttling into and out of their burrows, and emerging only for brief periods on to the soil surface to forage (Fig. 4.14) (Bennett et al. 1984). At this time, T_e exceeded 40°C (burrow temperature was only 27°C). The ground squirrel started to forage more consistently on the surface in the late afternoon (after about 17h30). Mean difference in T_e between parasol tails and prone tails between 09h15 and 17h30 was 5.6°C (maximum = 8.3°C).

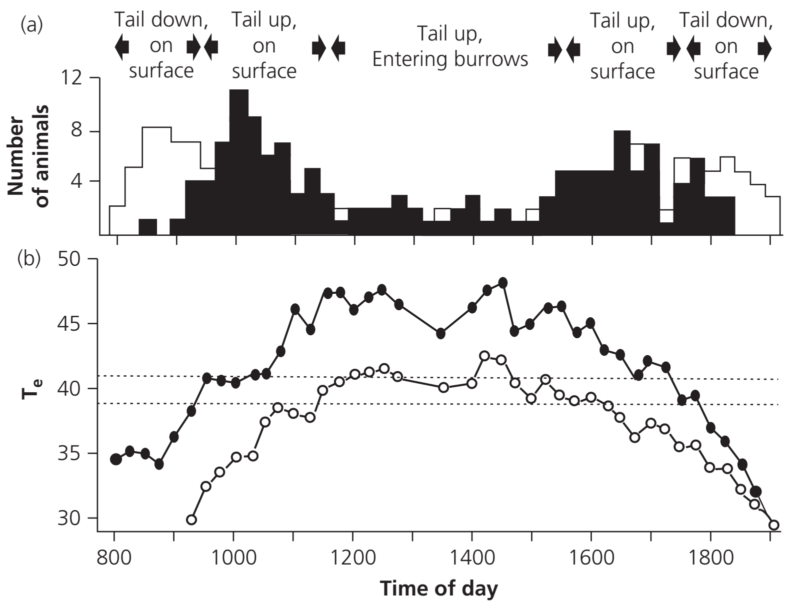

Fig. 4.14 (a, b) Between 09h15 and 11h30, squirrels usually raised their tails and faced their backs to the sun. After 11h30, most squirrels started disappearing from the surface, shuttling into and out of their burrows, emerging only for brief periods onto the soil surface to forage. Black columns = individuals with tails up over their backs; white columns = animals with tails down; black circles = model with the tail down; white circles = model with the tail up; dashed lines = approximate range of ambient temperatures that begins to elicit a rise in body temperature and salivation.

Source: From Bennett et al. (1984). With kind permission of University of Chicago Press.

4.1.4 Spider burrows and termite mounds

Two special types of burrows are the tubular structures used by burrowing spiders and termite mounds:

4.1.4.1 Burrowing spiders

Lubin and Henschel (1990) studied the spider *Seothyra henscheli* (Eresidae) that burrows beneath the Namib dunes. Burrows are web-lined and about 10–15 cm in depth, with a web capture surface. When a prey item (often an ant) becomes entangled in the capture web, the spider rushes to the surface to strike at and subsequently disentangle the prey. Thereafter, the spider removes the prey from the capture web and withdraws with it to the bottom of the burrow. This spider, in the heat of the day, 'shuttles' with the prey item, taking it down to the depths of the burrow, because the temperature at the surface can be as much as 70°C. Although the critical thermal maximum (CTMax) temperature of these spiders is high (about 49°C), if a burrow was only 5 cm deep or less, it would get too hot for these spiders. The most important part of shuttling is the post-strike retreat, which occurs when it gets too hot for the spider to spend time on the surface (Turner et al. 1993).

4.1.4.2 Termite mounds

Darlington (1987) considered there to be two basic types of macrotermite mound, open and closed. Darlington (1987) found that open mounds should function like a Venturi effect, where wind passing over the open colony forces air out of the colony as external air is drawn into the colony through termite entrance holes in the base of the mound. For a Venturi effect (better known as induced flow (Vogel 1994)) to work, there must be ventilation via holes in the ground and ventilation above the ground. A negative hydrostatic pressure gradient will result, so that air is drawn into the lower openings and out of the upper opening. Turner (1994) found just such an effect in a termite species of arid southern Africa, *Odontotermes transvaalensis*. On average, just 80 min of air circulation is needed for 95% of colony air to be exchanged with the surroundings.

Lüscher (1961) considered the closed macrotermite mound to work as an effect of the high metabolic rate of the termite colony. Specifically, the heat and humidity of the mound created by this high metabolic rate (estimated by Darlington et al. (1997) to be hundreds of watts) lowers the density of the air. The resulting buoyant forces drive the heat towards the chimney and exit channels (Fig. 4.15). Homeostasis of the mound is achieved when there is a link between circulation rate and colony metabolism. This is known as a 'thermosiphon effect' (Lüscher 1961). However, Turner (2001) studied the closed mound of *Macrotermes michaelseni* and found that it is a bit more complicated than Lüscher (1961) assumed. Turner (2001) found that wind is the primary factor determining nest ventilation and that tidal effects are driven by local variation in wind speed and direction. However, consistent with Lüscher's (1961) hypothesis, Turner (2001) found that metabolism-induced variation in buoyant forces may function with tidal forces to create homeostasis within the mound.

4.1.5 Physiological mechanisms of controlling heat gain

Birds and larger desert mammals that use evaporative cooling risk dehydrating because of the difficulty of finding sufficient drinking water. For mammals,

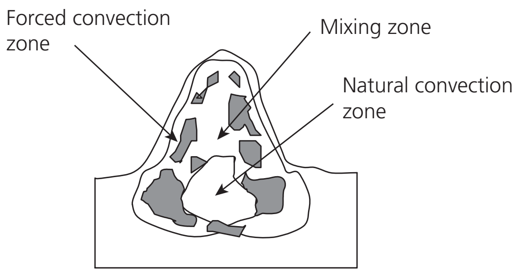

Fig. 4.15 Lüscher (1961) considered the closed macrotermite mound to work as an effect of the high metabolic rate of the termite colony. Specifically, the heat and humidity of the mound created by this high metabolic rate lowers the density of the air. The resulting buoyant forces drive the heat towards the chimney and exit channels. Homeostasis of the mound is achieved when there is a link between circulation rate and colony metabolism.

Source: From Turner (2001). With kind permission of University of Chicago Press.

evaporative heat loss includes panting and sweating. In small mammals and birds, the temperature of exhaled air is often lower than T_b, resulting in condensation of water on the nasal mucosa. While resting in their cool burrows during the heat of the day, small desert mammals rely on this mechanism for water conservation. However, for mammals and birds exposed to high T_a, the nasal countercurrent heat exchanger minimizes water loss, and so works against the need to increase heat loss by evaporation of water. The most important of these characteristics is the carotid *rete mirabile*, a maze of blood vessels that works similarly to the radiator of a vehicle. Warm blood flowing from the heart to the brain passes through a network of vessels surrounded by veins carrying blood already cooled through evaporation (in the nasal area). Heat is exchanged in this process and thus lowers the temperature of the blood to the brain. It is a very efficient way to protect the body and simultaneously avoid too much sweating, which has the result of fluid loss. In desert-dwelling pigeons, Pinshow et al. (1982) have shown that the *rete mirabile ophthalmicum* works by shunting warm blood to the curved outer surface of the eye, where it is cooled convectively and is then shunted back to the brain.

Some small organisms enter torpor (a lowering of T_b below T_a), either on a daily or on a seasonal basis. Torpor can be advantageous to mammals and birds because they reduce their requirements for energy and decrease cutaneous, respiratory, and excretory water loss (Lovegrove 2012). Certain mammalian taxa are more likely than others to enter torpor (Lovegrove 2012; Fig. 4.16). Torpor can be separated into hibernation (in winter cold periods), aestivation (to avoid heat), and short-term torpor. Ruf and Geiser (2015) found, in an analysis of mammals and birds, that heterothermic endotherms tended to be small while hibernators were significantly heavier than daily heterotherms. They also found that hibernators were also distributed at higher average latitudes (~35°C) than daily heterotherms (~25°C). Ruf and Geiser (2015) found that mean minimum torpor metabolic rate was ~35% of the basal

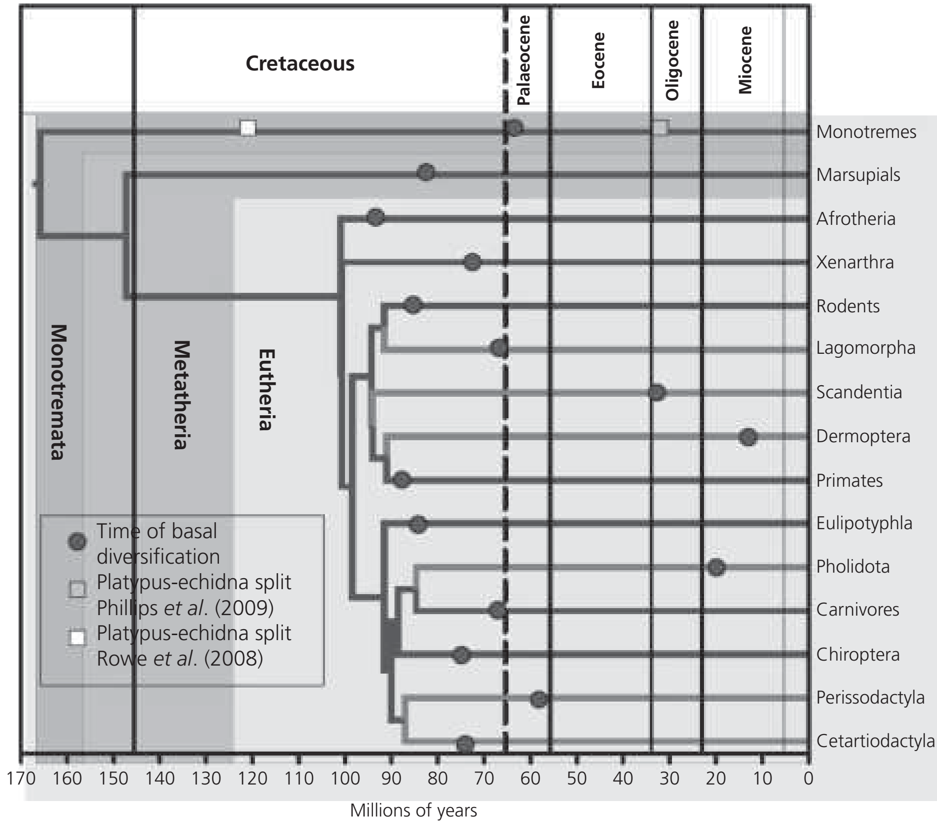

Fig. 4.16 Mammalian taxa that are most likely (dark lines) to enter torpor (Lovegrove 2012). The phylogeny and divergence dates of the terrestrial mammalian orders follow Bininda-Emonds et al. (2007). Dark branches represent orders in which heterothermy has been reported, whereas grey branches represent orders in which heterothermy has not been reported. Circles indicate the basal divergence date within each order.

Source: From Lovegrove (2012). With kind permission of Blackwell.

metabolic rate (BMR) in daily heterotherms but only 6% of BMR in hibernators. Their analysis strongly supported the view that hibernators and daily heterotherms are functionally distinct groups that probably have been subject to disruptive selection. These authors contend that the main physiological difference between daily torpor and hibernation is the control of entry into and arousal from torpor, which is governed by the circadian clock in daily heterotherms, with no apparent control in hibernators.

An interesting example of torpor occurs in the round-eared elephant shrew, *Macroscelides proboscideus* (Macroscelidea, Mammalia), which occurs in the arid parts of

South Africa, Botswana, and Namibia. Lovegrove et al. (1999) showed that torpor, which varied in duration from <1 h to about 18 h, was induced by food deprivation and not by low T_a. However, Vuarin and Henry (2014), in a review of torpor in mammals, found that most studies have relied on correlative evidence for the relationship between food deprivation and torpor. Manipulations of food availability that demonstrate the proximate role of food availability have been conducted in only five free-ranging heterotherm species. In an Australian study on one of those five heterotherm species, Munn et al. (2010) found that if a desert marsupial, the fat-tailed dunnart (*Sminthopsis crassicaudata*), is offered unpredictable levels of daily food, the fat-tailed dunnarts increased the frequency of daily torpor and length of bouts compared with animals offered *ad libitum* food (Fig. 4.17). However, when these animals were offered a predictable 70% food-restricted diet they did not enter torpor. Their data suggest that predictable food restriction may not be sufficient for evaluating the efficacy of torpor as a strategy for managing unpredictable climates but unpredictable changes induced torpor. Vuarin and Henry (2014) warn that several other metabolic constraints covary with food availability and can confound its effect. Shortage in water availability, the nutritional composition of food, or subsequent conversion of food in fat storage could be proximate drivers of heterothermy regulation, instead of food shortage. Social interactions, competition for food, and predation also probably have an effect on the relative magnitude of food shortage between individuals (Vuarin and Henry 2014).

Mzilikazi and Lovegrove (2004) have shown that arousal from torpor in *Macroscelides proboscideus* can be achieved by passive thermoregulation when the sun rises, as did Geiser (2004) in a review of Australian mammal species. Geiser (2004) found that basking is a common (but not the only) means of arousal from torpor. Tomlinson et al. (2007), for example, investigated the conditions under which the endemic

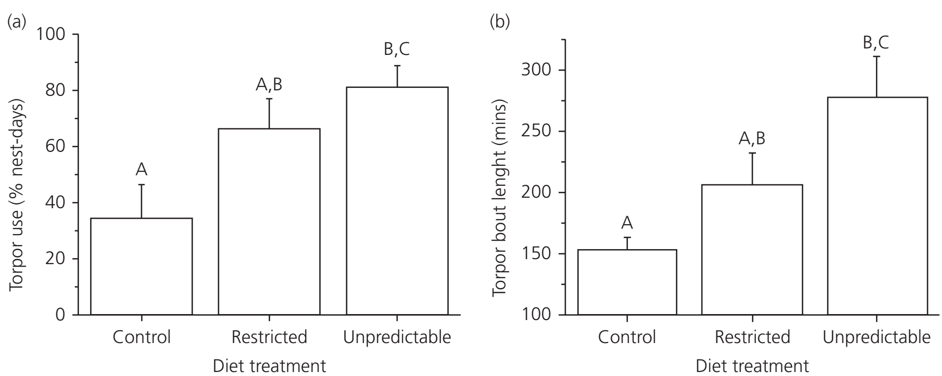

Fig. 4.17 Effects of diet restriction on (a) torpor frequency and (b) length of torpor in fat-tailed dunnarts. Different capital letters indicate significant differences among categories.

Source: From Munn et al. (2010). With kind permission of Springer.

Australian desert mouse, *Pseudomys hermannsburgensis*, aroused themselves from torpor. They found that this species became hypothermic at low ambient temperatures (T_b was about 17°C at T_a = 15°C) but they did not spontaneously arouse themselves by basking. However, they did survive and became normothermic (T_b = 33°C) if returned to room temperature (23°C).

Panting is an important cooling mechanism for foxes and other animals that chase prey. The fennec fox (*Fennecus zerda*), a species found in the Sahara Desert, is reputed to pant at 690 times per minute after chasing prey (Maloiy et al. 1982). Rüppell's foxes (*Vulpes rueppellii*) live in the Rub' al-Khali (the so-called 'Empty Quarter') of Arabia, the largest existing sand sea, which is an extremely arid desert with no permanent sources of drinking water. These foxes obtain all their water from food, supplemented by metabolic water production. As a result of their nocturnality, Rüppell's foxes might be expected to have a reduced total evaporative water loss (TEWL) in comparison to fox species living in mesic habitats. Resting in a den during the day would reduce TEWL, but Rüppell's foxes would have to travel long distances at night while hunting their prey, mainly rodents, birds, and arthropods, thereby increasing the need for evaporative cooling. Williams et al. (2002) measured TEWL of individual foxes at 35°C and found it to be about 50 g water day^{-1}, which is about 55% lower than allometric (body mass) expectations for other mammalian species. This was achieved by reducing either cutaneous or respiratory water loss (Williams et al. 2002).

Because birds of all sizes tolerate hot arid conditions, many physiologists (e.g. McNab 1966; Heinrich 1977) have considered that desert birds, being diurnal animals exposed to extremes of ambient temperature and aridity in deserts, are successful because they have higher T_b (41–2°C) than mammals, reducing their relative need for evaporative cooling. Also, because birds are uricotelic (they excrete uric acid rather than urea), relatively little water is required for the excretion of nitrogenous waste (see section 4.1, 'Evaders and evaporators'). However, Williams and Tieleman (2005) have shown that birds from deserts have not only a reduced rate of metabolism for their body sizes but also a smaller clutch size and slower nestling development than birds from mesic regions. They conclude from this that attributes of physiology are correlated with traits that directly affect reproductive success or fitness. These authors deny the widespread claim that birds are pre-adapted (= 'exaptation' *sensu* Gould and Vrba 1982) for desert life: *adaptations* are features that developed by natural selection for their current roles; *exaptations* include non-functional male nipples in mammals (Gould and Vrba 1982).

Many desert birds, particularly ground-nesting species, use panting for cooling, thereby incurring increased evaporative water loss. Female dune larks, *Certhilauda erythrochlamys*, incubating their eggs pant during midday to regulate their own body temperature and hence their eggs (Williams 2001). Crowned lapwings, *Vanellus coronatus* (Charadriiformes), are also ground nesters, as are desert sandgrouse (*Pterocles* spp., Pteroclidiformes) and, in addition to panting, they may also use gular fluttering, a rapid vibration of the floor of the mouth that provides rapid evaporative heat loss with up to 2°C cooling in the mouth (Hinsley et al. 1993; Downs and Ward 1997). *Pterocles* spp. can afford to lose water in this way, as these birds fly long distances every day to drink water from pools (Cade and Maclean 1967; Hinsley et al. 1993). Other birds such as desert larks do not show this behaviour because they rely entirely on water obtained from their food, so they cannot afford to lose so much water by evaporation (Williams 2001). Crowned lapwings do not drink but will pant or use gular fluttering on extreme occasions when forced to cool their eggs. A problem with panting and gular fluttering is that, while it achieves cooling by evaporative water loss, it can also result in an increase in CO_2 in the lungs, which leads to respiratory alkalosis (i.e. a change in acid–base balance) (Calder and Schmidt-Nielsen 1966). Larks do not usually nest in the open where they are exposed to direct sunlight and albedo (reflection of sunlight off ground surfaces), while plovers and sandgrouse do. Downs and Ward (1997) considered whether crowned lapwings raised themselves above their eggs to cool themselves or their eggs. Maclean (1967) had speculated that the eggs were cooled in double-banded coursers, *Rhinoptilus cursorius*, in the Kalahari Desert because the wind passing over the eggs would convectively cool them. However, Downs and Ward (1997) found that there was a greater cooling effect on the adults. Adult lapwings cooled themselves above the boundary layer and then sat back on their eggs, cooling the eggs in turn.

An additional unique adaptation of sandgrouse is the evolution of curled belly feathers. When they have young in their nests, males sometimes fly as much as 40 km to reach water. They stand in the water, and the feathers expand and collect water in the curls (Cade and Maclean 1967; Rijke 1972; Joubert and Maclean 1973) (Fig. 4.18). Thereafter, they drink water themselves and fly back to their chicks, who drink the water by stripping it from the belly feathers of the parent. Cade and Maclean (1967)

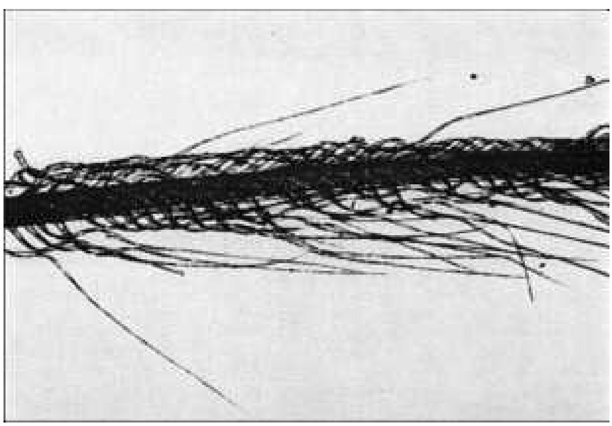

Fig. 4.18 Belly feather of a male Namaqua sandgrouse.

Source: Photo from Cade and Maclean (1967). With kind permission of the Cooper Ornithological Society.

found that male Namaqua sandgrouse could hold a mean of about 19 mg water.mg dry feather mass^{-1} while many other birds that they tested could only hold a mean of about 5–7 mg water.mg dry feather mass^{-1}.

4.2 Adaptations to handle unique situations

4.2.1 Salt glands in birds and reptiles

There are many species of marine birds that need to deal with the problem of excess seawater. This is done by using unique nasal glands called salt glands, which are effective transport epithelia for removing excess salt. Similar to the kidney, they work by using osmosis to remove salts through special glands in the nares. The same salt glands are possessed by a few taxa of desert birds. The desert orders with salt glands include Struthioniformes (ostriches), Gruiformes (including bustards), Charadriiformes (including lapwings, coursers, and plovers), Galliformes (recorded in the sand partridge *Ammoperdix heyi* only), Anseriformes (geese), Cuculiformes (roadrunner), Phoenicopteriformes (flamingos), and Falconiformes (raptors) (Maclean 1996). The production of excess salt mostly occurs as a result of attempting to reduce NaCl loads when extremely high T_a is experienced, such as the production of salt in the Australian pratincole, *Stiltia isabella* (Jesson and Maclean 1976), and inland dotterel, *Peltohyas australis* (Maclean 1976). High NaCl loads near saline lakes may also lead to the production of salt in these glands (Mahoney and Jehl 1985a, b). In raptors and the roadrunner, *Geococcyx californianus*, the birds incur a salt load from their (mostly) mammalian prey. This has been recorded in 16 Accipitridae species and 5 species of Falconidae (Maclean 1996). In the case of the gabar goshawk, *Micronisus gabar*, which lives in the arid areas of the Kalahari, Namib, and Karoo, a bird was observed to start secreting fluid from its external nares about 9 min after starting to eat a mouse (Cade and Greenwald 1966).

In addition to occurring in desert birds, some reptiles secrete salt through salt glands. This is known from several species in the Iguanidae, Agamidae (two species of large herbivorous *Uromastyx*), Scincidae (skinks), Xantusidae, Lacertidae, Teiidae, and Varanidae. In addition to secreting NaCl, some of these reptiles may also secrete K and the accompanying anion may either be Cl or bicarbonate. For example, Hazard (2001) found that *Dipsosaurus dorsalis*, an herbivorous desert lizard, only secreted increased levels of K and Cl; there was no response to increased levels of Na or bicarbonate. She concluded that this was due to the specificity of dietary K or Cl for these herbivorous lizards (Fig. 4.19).

4.2.2 Mammals that consume halophytes

Although salty areas are found in all deserts, there are relatively few mammal species that can tolerate these plants. A number of insect species, especially the leafhoppers (Cicadellidae, Insecta), have taken advantage of this niche. Nonetheless,

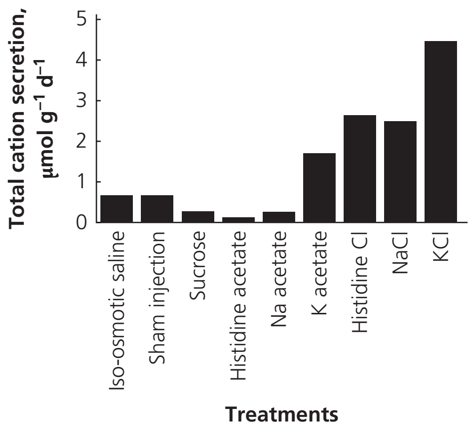

Fig. 4.19 Hazard (2001) examined the extrinsic factors (salts and other loads) and intrinsic factors (hormones and neurotransmitters) controlling rate and composition of secretion by the desert iguana (*Dipsosaurus dorsalis)*, an herbivorous desert lizard. Desert iguanas normally secrete potassium chloride to help eliminate the high amounts of potassium found in the desert plants they eat. Other vertebrate salt glands secrete in response to any osmotic challenge (e.g. NaCl, sucrose). Desert iguana salt glands respond specifically to increases in plasma potassium or chloride. They do not respond to sodium alone or other osmotic challenges (sucrose, histidine acetate). Effects of potassium and chloride appear to be additive.

Source: From Hazard (2001). With kind permission of University of Chicago Press.

halophytic plants have very negative water potentials, which mean that they take up large amounts of water and, in doing so, also take up large amounts of salts. In some plant species (e.g. *Atriplex* (Chenopodiaceae)) that are green and succulent (West 1983; Mares et al. 1997), there are specialized salt glands on the leaves where this salt is deposited. A small number of small mammal species have developed ways of avoiding the salts. In the Negev Desert, the fat sand rat, *Psammomys obesus*, removes the salt from the leaves using their teeth (Degen 1988). Similar devices have been employed by the North American chisel-toothed kangaroo rat, *Dipodomys microps*, and the South American vizcacha rat, *Tympanoctomys barrerae*. In this latter species, a native of the Monte Desert, an additional feature is the use of bristle-like hairs on either side of the mouth that occlude with the lower incisors and act to remove the salt from *Atriplex* salt glands (Fig. 4.20). The kidney of *Tympanoctomys barrerae* is similar to that of *Psammomys obesus*, in that it has a long renal papilla, which is a structural adaptation that permits it to act as a countercurrent filter to more effectively remove salts (Ojeda et al. 1999). An additional problem encountered by *Psammomys obesus* is that *Atriplex halimus* also contains very high levels of calcium oxalate. The way that *Psammomys obesus* deals with this problem is by bacterial degradation of oxalates. The intake ratio of oxalate:calcium is 4.5:1 while the excreta of *Psammomys obesus* is 1.25:1 and is probably mostly digested by intestinal bacteria (Palgi et al. 2005).

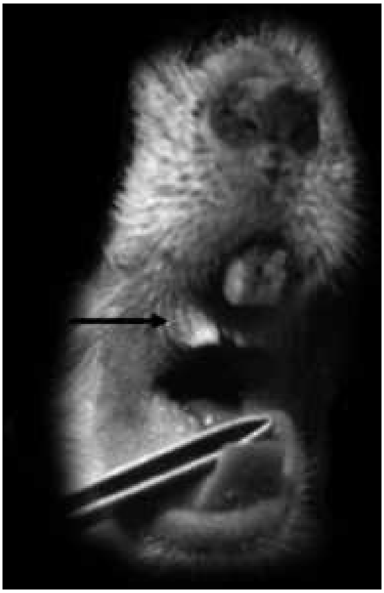

Fig. 4.20 South American vizcacha rat, *Tympanoctomys barrerae*, uses bristle-like hairs (see arrow) on either side of the mouth to remove the salt from *Atriplex* salt glands.

Source: From Mares et al. (1997). Copyright: American Institute of Biological Sciences.

4.2.3 Animals in temporary pools

A number of different animals live in unique communities in the small, ephemeral water pools that collect in deserts after rains. They may be divided into three groups, based on their responses to droughts. The *drought escapers* are winged insects, amphibians, and some invertebrates that use these water bodies when present, but escape by migration or other means when the water dries up (Dayton and Fitzgerald 1995; Blaustein and Margalit 1996; Suhling et al. 2004; Bogan et al. 2014). In the cases of crustacean larvae, such as tadpole, fairy, and clam shrimps, adults must lay drought-tolerant eggs before the pool dries up. The adults then die (Bogan et al. 2014). *Drought resistors* include snails and mites and have a dormant stage that is resistant to desiccation (Davis et al. 2013). They have a waterproof layer such as an exoskeleton or shell that prevents the body tissues from losing too much water. They are also capable of burrowing into the fine mud that seals the bottoms of many pools. *Drought tolerators* such as rotifers can tolerate very high levels of desiccation. This is known as cryptobiosis (Jönsson and Järemo 2003). These animals can rehydrate themselves very quickly and can be fully functional in as little as 30 min (Williams 1985). Water is not the only cue, because these organisms can also respond to other factors such as salinity, oxygen content, temperature, and other physical and chemical factors in the water (Davis et al. 2013). Davis et al. (2013) differentiate between ecological refuges and evolutionary refugia in Australian arid zones. Ecological refuges can vary across space and time, depending on the dispersal abilities of aquatic taxa and the geographical proximity and hydrological connectivity of aquatic habitats. The most important ecological refuges are the perennial waterbodies (both groundwater and surface-water fed) that support obligate aquatic organisms such as desert fish. These species will persist where suitable habitats are available and dispersal pathways are maintained. Evolutionary refugia, by contrast, are characterized as permanent, groundwater-dependent habitats (subterranean aquifers and springs) that support relict populations that are separated from other populations and are likely to undergo speciation or have speciated already (short-range endemics). For very mobile species (invertebrates with an aerial dispersal phase) evolutionary refugia may also act as ecological refuges. Evolutionary refugia, unlike ecological refuges, are likely future refugia because their water source (groundwater) is decoupled from local precipitation because they are able to access groundwater.

4.3 Endurers

The best-known examples of desert endurers include the camel, the oryx, and desert sheep. In fact, most desert endurers are large mammals. However, this is not entirely correct. For example, ants are also known as endurers despite their small size.

4.3.1 Ants

Ants are capable of tolerating some of the highest temperatures (Marsh 1985; Wehner et al. 1992). In the Sahara Desert, *Cataglyphis* species forage at body temperatures above 50°C. In the two *Cataglyphis* species measured the critical thermal maxima are at 53.6 + 0.8°C for *Cataglyphis bombycina* and 55.1 + 1.1°C for *Cataglyphis bicolor*. Shi et al. (2015) found that the conspicuous silvery appearance of *Cataglyphis bombycina* ants is created by a dense array of uniquely shaped triangular hairs with two thermoregulatory effects. They enhance not only the reflectivity of the ant's body surface in the visible and near-infrared range of the spectrum, where solar radiation culminates, but also the emissivity of the ant in the mid-infrared. The latter effect enables the animals to efficiently dissipate heat back to the surroundings via black-body radiation under full daylight conditions.

Gehring and Wehner (1995) analysed the synthesis and accumulation of HSPs in *Cataglyphis bombycina* and compared these HSPs to those of *Formica polyctena*, an ant living in mesic climates, and to two *Drosophila* species, the cosmopolitan *Drosophila melanogaster* and the Palaearctic *Drosophila ambigua*. In *Cataglyphis bombycina*, protein synthesis continues at temperatures up to 45°C as compared to 39°C for *Formica* and *Drosophila*. The two *Drosophila* species differ with respect to their maximal induction of HSP synthesis and accumulation by 3–4°C. In contrast, *Cataglyphis bombycina* and *Formica polyctena* ant species accumulate HSPs prior to their exposure to heat. In *Cataglyphis bombycina*, the temperature of maximal

HSP induction by *de novo* protein synthesis is only 2°C higher than in the mesic ant, *Formica polyctena*. These findings are interpreted as pre-adaptation (i.e. *exaptation sensu* Gould and Vrba 1982) of the ants prior to exposure to high temperatures.

4.3.2 Large mammals

The relatively low surface area:volume ratio of large mammals means that they have more difficulty than small animals in losing heat from the body at high T_a. Mammalian and avian endurers (such as ostriches, which are also large and often live in deserts) are too large to shelter in burrows and, if no shade is available, they may be forced to remain exposed to solar radiation during the day. The hair and feathers of large desert mammals and birds can play an important role in insulation, from both solar heat and nocturnal cold.

Large mammals tend to be inactive during the hottest part of the day, thereby reducing metabolic heat production. Hartmann's mountain zebras, *Equus zebra hartmannae* (Namib Desert) (Fig. 4.21), and oryx (also known as gemsbok), *Oryx gazella* (Namib, Kalahari, and Karoo deserts), orient their bodies with the sun during the day. Hartmann's mountain zebras will climb eastward-facing slopes to absorb the sun's morning warmth. As the day progresses they find shade. The oryx of the southern African deserts commonly stands on the top of open dunes in the heat of the day to catch the cool winds passing over them. Nonetheless, this species is also known to cover great distances, even at noon (Fig. 4.22). In Africa's Namib Desert, Hartmann's mountain zebras have been observed to sniff out water on the surface of dry river beds. They paw at the ground with their hooves to get to water that is sometimes 1 m below the surface. By doing so, these zebras benefit other desert-dwelling animals. It has also been mentioned that Hartmann's mountain zebras can go without water for 4 days. In contrast, the Asiatic wild ass, *Equus hemionus*, in the Negev Desert (Israel) must drink daily (Saltz et al. 2000).

Fig. 4.21 Hartmann's mountain zebra in the Namib Desert.
Source: Photo used by Creative Commons licence.

Fig. 4.22 Oryx in the Namib Desert.
Source: Photo used by Creative Commons licence.

The Arabian oryx, *Oryx leucoryx*, lives in the Arabian desert (Fig. 11.11), which includes areas where free-standing water is rarely, if ever, available. Where possible, the Arabian oryx spends time sitting in the shade of evergreen trees during the hottest part of the day. On hot days, these oryx also dig into the sand, exposing cool sand below the surface and sit in the depressions. Body heat is lost to the cooler sand by conduction (Williams et al. 2001; Ostrowski et al. 2003). Arabian oryx forage at night during the summer, avoiding exposure to high T_a and intense solar radiation (Williams et al. 2001). They feed on grasses and rely on the water content of the plants for their intake of water (Ostrowski et al. 2003). BMR and TEWL at 30°C were measured in Arabian oryx living in the Arabian desert, as were field metabolic rates (FMR) and field water influx rates (a measure of water intake) using the doubly labelled water technique (Williams et al. 2001). In the summer, when grasses were parched, field metabolic rates of free-ranging oryx were 11,076 kJ day^{-1} in contrast to 22,081 kJ day^{-1} in spring, after rains. Williams et al. (2001) suggest that Arabian oryx cut their energy expenditure in summer by changing both behaviour and physiology. In summer, oryx forage at night and rest during the day. After spring rains, increased energy expenditure may occur because these animals must walk longer distances to forage, and also these animals have higher costs of thermoregulation because of reduced T_a (Williams et al. 2001).

At rest, the body temperature of normal healthy dromedary (one-humped) camels, *Camelus dromedarius* (Fig. 4.23), can vary from about 34 to >40°C (Schmidt-Nielsen

Fig. 4.23 Head of a camel.

Source: Photo by Keven Law under Creative Commons licence.

et al. 1956). This means that, in contrast to popular expectation, these animals are essentially heterotherms. However, temperature regulation in this species depends heavily on the availability of water. In summer, the diurnal variations in a camel deprived of drinking water may exceed 6°C, but in animals with free access to water the variations are similar to those found in the winter (about 2°C). Variation in T_b has important consequences for water conservation because:

1. An increase in T_b means that heat is stored in the body instead of being dissipated by evaporation of water. At night the excess heat can be given off without expenditure of water.
2. The high T_b means that heat gain from the hot environment is reduced because the temperature gradient is reduced. According to the Stefan–Boltzmann law, a body under constant conditions changes temperature to match that of its surroundings at a rate that is equal to the fourth power of the difference between them.

Heat regulation in camels occurs by evaporation from the skin surface (sweating), with no apparent increase in respiratory rate or panting. Evaporation from isolated skin areas increases linearly with increased heat load at a critical temperature of around 35°C. The fur of the camel is an efficient barrier against heat gain from the environment. Water expenditure is about 50% higher in camels that have been shorn (Schmidt-Nielsen et al. 1956).

Schmidt-Nielsen et al. (1971, 1981) showed that a 17% weight loss due to dehydration in a camel was accompanied by a 9% reduction in plasma volume and a 38% fluid loss from the gut. A camel has up to 75 L of fluid in its rumen (85% of which is water) and another 8 L in the intestine. The 38% of water loss in the gut is therefore about 30 L, which minimizes strain on the blood circulation during dehydration.

The camel can cope with up to 30% water loss, meaning that camel tissues are more resistant to high osmotic pressures than those of many animals. When provided with water after such a high level of dehydration, the camel can drink rapidly, taking in up to 200 L of water in just a few minutes. Much of the water taken in is stored temporarily in the gut, preventing excessive dilution of the blood, which would be harmful.

Schmidt-Nielsen et al.'s (1981) study improved our understanding of the common perceptions that camels store free water in the rumen and utilize water derived from metabolism of the lipids released from adipose tissue in the hump. Although camels have a great deal of water in the rumen and intestine, it is proportionately no more than is present in other ruminants. The oxidation of 1 g fat yields 1.07 g water; thus, a 40-kg hump could yield 43 L of water that can be drawn on during a long journey. However, because this mechanism requires oxygen that can only be obtained by ventilating the lungs, there must be a net loss of water from the respiratory tract when the camel breathes dry air. Whether the fat reserves make a positive or negative contribution to the animal's overall water balance therefore depends on conditions in the upper respiratory tract.

In general, long limbs, tails, or necks provide large surface areas from which heat can be dissipated, and behaviour patterns may maximize loss of heat from these areas (Crawford and Schmidt-Nielsen 1967). The ostrich, *Struthio camelus*, is the largest living bird, weighing between 70 and 150 kg. Ostriches forage during the day, selecting plants with high water content during times of water shortage (Williams et al. 1993). The long, naked neck and legs of the ostrich provide a large surface area for convective and radiative cooling (Crawford and Schmidt-Nielsen 1967). The ostrich uses behaviour to enhance the cooling effects of feather erection at a high ambient temperature and incident solar radiation (Sauer and Sauer 1967; Louw et al. 1969). Sparsely distributed long feathers on the dorsal surface of the bird erect in response to warming of the skin, thereby increasing the thickness of the insulation between solar radiation and skin. The gaps between the feathers allow through air movements, which cool the skin by convection (Sauer and Sauer 1967; Louw et al. 1969). The birds supplement the physiological response during the hottest part of the day by orientating themselves towards the sun and bowing their wings away from the thorax, forming an 'umbrella' which shades the exposed thorax. The naked skin of the thorax acts as a surface for heat loss by both radiation and convection (Crawford and Schmidt-Nielsen 1967). At night when ambient temperatures decline, ostriches conserve heat by folding their wings close to the thorax and tucking their legs under the body while they sit on the ground (Sauer and Sauer 1967). The dorsal feathers respond to low T_a by flattening and interlocking, which traps an insulating layer of air next to the skin and keeps most of the skin at 34.5°C (Louw et al. 1969).

Certain large lizard species behave similarly to endurers, but they are evaders and evaporators too, showing that we should not apply this classification too strictly. One of the more interesting adaptations, which also occurs in aquatic amphibians and turtles, occurs in the Sonoran Desert-dwelling Gila monsters, *Heloderma suspectum*

(Davis and DeNardo 2007). These lizards use their urinary bladders to store dilute urine, drawing on it to buffer plasma osmolality when they are dehydrated or food limited. Plasma osmolality increased 2.5 times faster when their urinary bladders were empty. These large lizards (mass = 350–600 g) could either draw on drinking (which provides a more immediate osmotic benefit) or use water stored in their urinary bladders within 24 h.

4.4 Removing the effects of phylogeny

There are several animal taxa for which suitable, phylogenetically controlled analyses have been conducted. This means that the effects of phylogeny, which may be considerable, have been removed (Felsenstein 1985; Garland et al. 1992). Removing the effects of phylogeny allows one to test whether an adaptation has occurred. Otherwise, it is possible that lack of statistical independence (pseudoreplication) could occur because characters may evolve by chance alone or because of phylogenetic inertia (Felsenstein 1985; Pagel 1994). For example, one might find that a trait is considered a desert adaptation because many desert-dwelling species possess it and non-desert-dwelling species do not. However, if there are many desert-dwelling species in a particular part of a clade, then this character may have evolved by chance alone. Here we will consider examples from phylogenetically controlled studies on ectothermic invertebrates, endothermic birds, and endothermic marsupial mammals.

4.4.1 Insects (tenebrionid beetles)

In the Namib Desert, tenebrionid beetle species (also known as darkling beetles) are particularly common. There are 13 species in the genus *Onymacris* that are very abundant. Ward and Seely (1996b) tested a number of hypotheses that relate to the physiology and associated behaviour of these species:

1. Preferred body temperatures (the body temperature that a beetle prefers to be active at; determined in a circular thermal gradient) closely match the body temperatures (T_b) actually attained in the field. It has been shown by Roberts et al. (1991) that there is a correlation between preferred and field T_b ($r^2 = 0.8$), without removing the effects of phylogeny. Preferred T_b values should have evolved to match the temperatures at which an animal is most energetically efficient (Huey and Bennett 1987). Furthermore, Heinrich (1993) predicted that the extremes of temperature, the critical thermal maxima (CTMax) and minima (CTMin), are key adaptations because it is the extremes of temperature that exert the strongest selection pressures. Thus, Ward and Seely (1996a) also examined relationships among CTMax, CTMin, and preferred and attained field T_b.
2. Desert beetles have evolved longer legs (relative to their body lengths) to enable them to 'stilt' (Penrith 1984) (see Fig. 4.24 for an example of this in *Onymacris unguicularis*). This means that extending their legs gets them out of the hot

boundary layer of air that usually envelopes the ground. For example, Medvedev (1965) found that tenebrionid beetles could lower their body temperatures between 3°C and 21°C in the Kara Kum Desert of Turkmenistan.

3. Wax blooms are more likely to occur in desert than in coastal populations or species (McClain et al. 1985) (Figs. 4.4 and 4.25). The wax bloom is an effective cuticular barrier to limit evaporative water loss (Hadley 1970; McClain et al. 1985).
4. Fog basking allows some *Onymacris* species to take advantage of the thick advective fogs that carpet the Namib from the sea (Fig. 4.26). Hamilton and Seely (1976) and Seely et al. (1983) found that two beetle species, *Onymacris unguicularis* and *Onymacris bicolor*, climbed to the top of a dune and allowed the fog to condense on their abdomens and drip down into their mouths. Parker and Lawrence (2001) and Zhai et al. (2006) found that this pattern in Namib Desert darkling beetles was due to alternating hydrophobic and hydrophilic surfaces on their fused elytra. One would expect that coastal species would be more likely to possess this behaviour because fogs are coastal.
5. Some species have a white abdomen (Fig. 4.27). Ward and Seely (1996b) tested whether these species were more likely to have evolved in desert than in coastal regions (Fig. 4.28).

After removing the effects of phylogeny, Ward and Seely (1996a) found that preferred T_b and actual T_b attained in the field were well matched, indicating perfect coadaptation. However, contra Heinrich (1993), they found no correlation among CTMax, CTMin, and preferred and attained T_b. In another study, Ward (1991) tested whether there was any support for Hamilton's (1975) 'maxithermy' hypothesis. Hamilton (1975) had suggested that desert beetles were mostly black to maximize thermal gain, which would allow them maximize efficiency of food intake over a short time period. Ward (1991) surmised that, if this were to be correct, starving the beetles (of three species) should lead to their preference for progressively lower temperatures. However, the beetles preferred the same (high) temperatures, regardless of the degree of starvation. This is inconsistent with both Hamilton's (1975) and

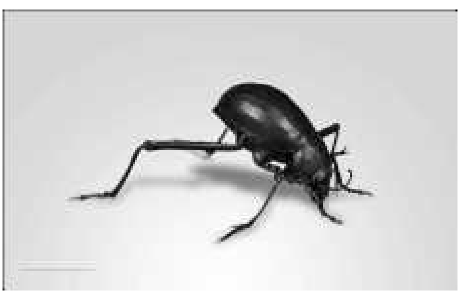

Fig. 4.24 Long legs of *Onymacris unguicularis*. This feature makes it easy for this species to engage in stilting behaviour.

Source: Photo by Didier Descouens (Museum of Toulouse, France) under the Creative Commons Licence.

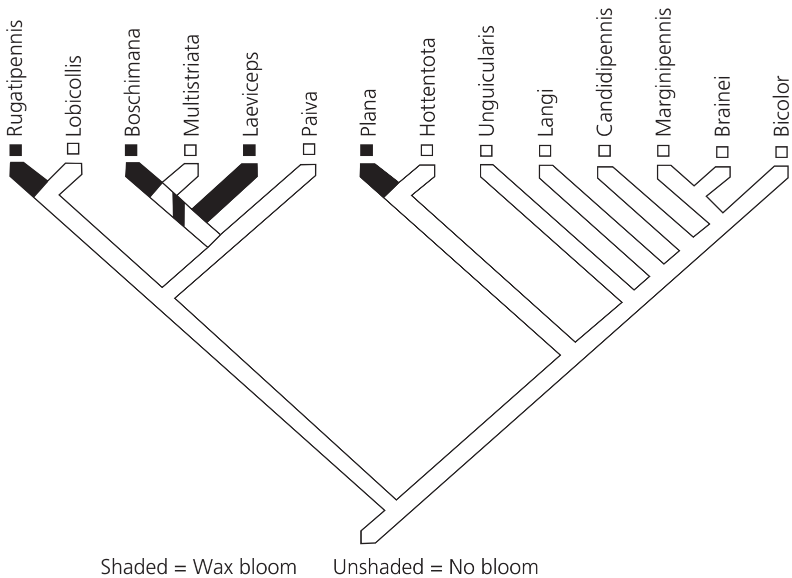

Fig. 4.25 Phylogeny of *Onymacris* with wax blooms. Hatch = uncertain origin of wax bloom.
Source: From Ward and Seely (1996b). With kind permission of Blackwell.

Heinrich's (1977, 1993) hypotheses. A possible reason why these beetles do not show strong selection for critical thermal extremes is that they only emerge from beneath the sand when CTMin is exceeded (Seely and Mitchell 1987) and descend beneath it before CTMax is exceeded or climb bushes to avoid the heat, moving off the hot sand (Ward and Seely 1996c). Their preferences for high T_b are still poorly understood.

In the case of fog basking, Ward and Seely (1996b) showed that it had evolved on two separate occasions and, thus, constitutes an adaptation to desert conditions. Similarly, they found that the wax bloom was indeed an adaptive characteristic, as

Fig. 4.26 Fog basking by the Namib tenebrionid beetle, *Onymacris unguicularis*.
Source: With kind permission of the Desert Research Foundation of Namibia.

Fig. 4.27 Photo of white *Stenocara eburnea*, near Swakopmund, Namibia.
Source: Photo by WBodi on iSpot SANBI.

had been claimed by McClain et al. (1985). However, the loss of the wax bloom in *Onymacris multistriata* and in one subspecies of *Onymacris, Onymacris rugatipennis rugatipennis* (it does occur in another desert subspecies, *Onymacris rugatipennis albotessalata*), both of which occur in the desert interior, is perplexing.

Ward and Seely (1996b) found no support for stilting as an adaptive characteristic in this genus. This may occur because thermal mixing of the boundary layer occurs. Also, small organisms such as beetles are known to be convectively coupled and not radiation coupled (Gates 2003). This means that wind speed affects their T_b more than radiation. A study by Turner and Lombard (1991) showed that beetle colour had no effect on T_b. Interestingly, Ward and Seely (1996b) found that desert interior species

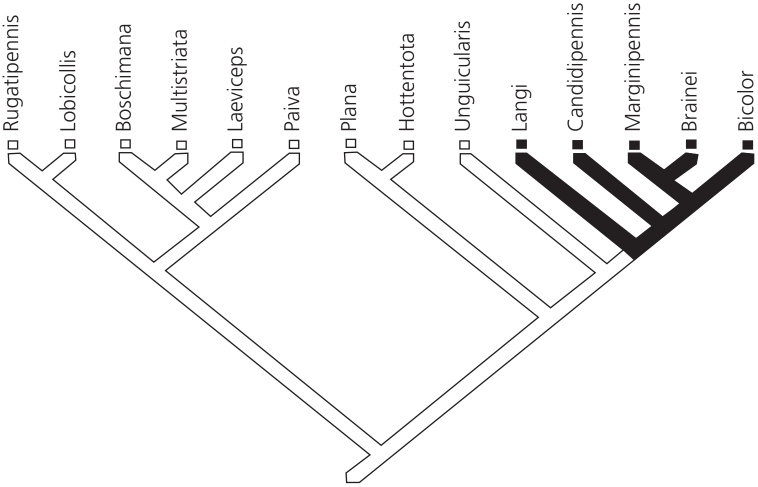

Fig. 4.28 Phylogeny of *Onymacris* with white abdomen. Black = white abdomen.
Source: From Ward and Seely (1996b). With kind permission of Blackwell.

had longer legs and coastal species had shorter legs than expected by chance. They suggested that a possible explanation for this was that long legs were ancestral and that there was little selection against them. However, tenebrionid beetles living on a sand substrate other than their own often had broken leg segments, suggesting that there was some selection against long legs (Koch 1962). A more parsimonious explanation could simply be that, if long legs were not needed, they would lose this characteristic.

Ward and Seely (1996b) showed that all white species had evolved from a single node (Fig. 4.28) and, thus, no claim could be made about unique, independent events. Moreover, white abdomens occurred in the coastal and not the desert interior species, contrary to the prediction.

In summary, Ward and Seely (1996b) showed that there were some characteristics that could be considered to be adaptive, others that were unlikely to be, and a few that showed some interesting trends worthy of further investigation. Most importantly, perhaps, not all such patterns would have been apparent had a conventional analysis been attempted. A more recent molecular phylogeny of three mitochondrial and three nuclear genes for the genus *Onymacris* has been developed (Lamb and Bond 2013). They found that there was paraphyly with *Physadesmia* and the 'white' taxa of *Onymacris*. One effect of this would be that *Physadesmia* is no longer considered a suitable outgroup for T_b comparisons and would have to be replaced with another taxon such as *Eustolopus*. Nonetheless, the earlier-mentioned hypotheses could be compared to Lamb and Bond's (2013) phylogeny to ascertain whether these adaptive hypotheses are still supported.

4.4.2 Birds

Using a study based on independent phylogenetic contrasts, Tieleman et al. (2003a) compared 22 species of larks with regard to the BMR and TEWL of arid and mesic species. For 12 lark species, they found that differences in body mass explained more of the variance in BMR (53%) and TEWL (72%) than aridity alone (38 and 15%, respectively). Nonetheless, a decreasing value of BMR (Fig. 4.29) and TEWL

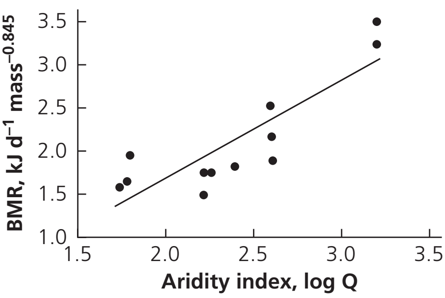

Fig. 4.29 Mass-adjusted basal metabolic rates (BMR) of 12 species of larks as a function of environmental aridity; log *Q* has low values when hot and dry and high values when it is wet and moist.

Source: From Tieleman et al. (2003a). With kind permission of the Royal Society of London.

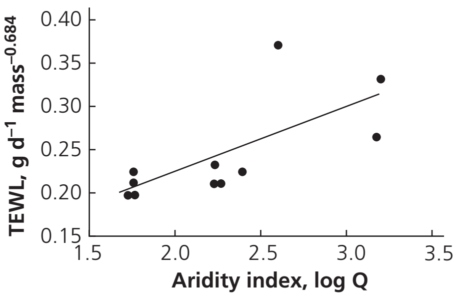

Fig. 4.30 Mass-adjusted total evaporative water loss (TEWL) of 12 species of larks as a function of environmental aridity; log *Q* has low values when it is hot and dry and high values when it is cool and moist.

Source: From Tieleman et al. (2003a). With kind permission of the Royal Society of London.

(Fig. 4.30) with increasing aridity was found after the effects of body mass had been removed. Interspecific correlations between the phenotype and the environment can be explained by adaptation via the process of natural selection or they may be a consequence of phenotypic plasticity. Phenotypic plasticity in desert birds may occur as acclimation to the local environment in adults or through restricted access to food as juveniles (ontogeny effect). In other studies, Tieleman et al. (2002, 2003b) found that there was no effect of restricted access to food, acclimation, or photoperiod and, therefore, Tieleman et al. (2003a) conclude that natural selection is the major selective force.

4.4.3 Marsupial mammals

A number of studies have shown differences in the metabolism of arid and mesic small mammal species. For example, studies by Murie (1961) and McNab and Morrison (1963) showed significant differences in the metabolism of arid and mesic populations of *Peromyscus* species. Furthermore, in a literature review of BMR of 487 mammal species of a wide range of body sizes, Lovegrove (2000) showed significant differences between xeric and mesic species, with lower BMR values per unit body mass for xeric species, which was especially notable for small mammals.

Withers et al. (2006) analysed body temperature (T_b), basal metabolic rate, and evaporative water loss (EWL) of marsupials in Australia and South America by conventional and phylogenetically corrected regression. Allometric effects for body size were substantial for BMR and EWL but not T_b. There was a strong phylogenetic signal for mass and all physiological traits, indicating that phylogeny was an important explanatory variable for these traits. A significant phylogenetic signal remained for BMR and EWL even after accounting for the highly significant phylogenetic signal of body mass. The allometric residuals for T_b were lower for marsupials from arid environments (high T_a and more variable rainfall) than from mesic environments. Withers et al. (2006) indicate that this lower T_b may result in increased energy and water savings in an arid environment with low productivity and high variability in rainfall.

The allometric slope for BMR of marsupials was 0.72–0.75 (Withers et al. 2006). Arid species (<250 mm annual rainfall) had significantly lower conventional BMR residuals than mesic species, but there was no relationship with diet. There was also a significant effect after the effects of phylogeny were removed. Residuals were consistently related to aridity and rainfall variability, with species from arid and variable rainfall habitats having a low BMR, presumably to conserve energy in a low-productivity environment. Interestingly, Rezende et al. (2004) found no significant effect of climate on BMR for another clade, the rodents, for both conventional and phylogenetic analyses.

The allometric slope for EWL for marsupials was 0.68–0.73 (Withers et al. 2006). EWL residuals were significant for both conventional analysis and phylogenetic corrections for rainfall variability but not for climate per se. EWL residuals for marsupials presumably facilitate maintenance of water balance during dry periods (Withers et al. 2006).

5 The Role of Competition and Facilitation in Structuring Desert Communities

Although abiotic factors are crucial to ensure survival in desert habitats, there are very important effects of competition and facilitation among both plants and animals (Tielbörger and Kadmon 2000; Goldberg et al. 2001; Adondakis and Venable 2004; Facelli et al. 2005; Wasserberg et al. 2007; Kotler et al. 2010). This chapter will focus on some of the key competitive and facilitative interactions among desert organisms, drawn from a wide range of studies in several deserts. I shall also consider the interesting possible causes of the formation of repeated circular and striped vegetation patterns that may be related to competition for water and, perhaps, nutrients.

5.1 Plant communities

Goldberg and Novoplansky (1997) have proposed a general schema for understanding the potential role of competition in plant communities. They call this the two-phase resource pulse hypothesis. Resources come in pulses, varying considerably in the duration of pulse availability (Chesson et al. 2004). Specifically, when a soil resource such as water and/or nutrients are limiting, the ability of individuals to monopolize resources by competitive ability (*sensu* Grime 1977) will occur during pulses of resource availability—of either water itself (the most limiting factor) or nutrients (which are linked to water availability)—depending on their abilities to suppress growth (termed competitive effect; *sensu* Goldberg 1990) or to avoid suppression themselves (termed competitive response; *sensu* Goldberg 1990). Interpulse periods are important, too, as the ability of plants to survive and, therefore, to persist during these periods (termed stress tolerance by Grime 1977) depends on how much resource is available. If the low level of resources is affected by plant density or abundance, then competition will still be important. If not, for example, if there are other causes of resource loss unrelated to competition such as evaporation, leaching, volatilization, and drainage, then competition will be unimportant. These are key issues of what Goldberg and Novoplansky (1997) and Craine (2005, 2007) termed the Grime–Tilman debate. Grime (1977) considered stress tolerance to be the most important factor (i.e. abiotic factors are more important), whereas

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Tilman (1982, 1988) considered competition to be important regardless of (or even particularly because of) low levels of water and/or nutrients. The magnitude of interactions will depend on the level of resources available between pulses that affect survival and the amount of resources available during resource pulses that facilitate growth. The most probable relationship is a positive correlation, so that competition would result in fewer resources during pulse periods, thereby reducing growth, and would also reduce survival during interpulse periods. In these circumstances, competition is likely to be important (as Tilman (1988 would predict). If, however, there is no relationship or a negative correlation between competition during resource pulses and during interpulse periods, and there is little or no relationship between resource availability and vegetation presence or abundance, then stress tolerance (*sensu* Grime 1977) is more likely to be important.

5.1.1 Annual plant communities

An interesting approach to the study of desert annuals was undertaken by Goldberg et al. (2001). Instead of focusing on the density of a single species at a time, Goldberg et al. (2001) noticed that density-dependent regulation should occur at the level of the whole community, especially where these plants occur in mixed-species groups as is so commonly the case. They examined the effects on different life history stages to determine whether similar responses were detected. Goldberg et al. (2001) constructed semi-natural communities of desert annuals in the Negev Desert of Israel, which were composed of all the constituent species in the same relative proportions as found in the natural habitat. These experimental communities were planted at a range of densities that were both far less than and far greater than natural field densities. Goldberg et al. (2001) demonstrated evidence of community-level density dependence. Exploitation competition should be the most common form of competition in plants because dominant plant species remove resources such as nutrients more quickly than subordinate species by exploitation (Tilman 1982, 1988). Interference competition could occur, but it is a little harder to understand because it could only really occur by allelopathy (e.g. negative effects of some toxin in the soil) or by other non-uptake mechanisms (*sensu* Goldberg 1990) such as attraction of natural herbivores. Exploitation competition was shown most clearly with regard to the growth phase of the experiment. At the survival stage, the effects were highly variable, but negative effects of density were quite rare. Rather, there were either positive (facilitation) or no significant effects of increasing density. They could not ascribe this to nurse-plant effects (see section 5.1.4, 'Facilitation and nurse-plant effects') because the plants were too similar in size, but could conclude that exploitation competition was unimportant at the survival stage. In their study, Goldberg et al. (2001) found that annual graminoids were superior competitors to dicotyledonous plants at the emergence and survival stages. However, the two growth forms did not differ in competitive ability for growth or final size. Nonetheless, dicots were, on average, heavier in biomass. Consistent with the former result, grasses are always the numerical dominants, but they are also biomass dominants in the source communities. How the latter might occur in nature was not determined.

Chesson (2000) has considered there to be a temporal mechanism by which a number of species can coexist, called a lottery model. Specifically, he estimated the contribution of temporal niches based on both among-year and within-year temporal niches in persistence and coexistence. For this mechanism to work, plants must increase when rare (Fig. 5.1), countering tendencies to local extinction and promoting species diversity. In the Sonoran Desert of North America, Pantastico-Caldas and Venable (1993), Pake and Venable (1995, 1996), and Adondakis and Venable (2004), as well as Facelli et al. (2005) in chenopod shrublands of south Australia, have shown that there is sufficient variation within years in the fraction of seedlings that germinate and that there is little correlation within years in terms of the species' germination responses (see also Chesson and Huntly 1989). This provides the species with slightly different temporal windows combined with the buffering effect of delayed germination. Chesson (2000) termed this the storage effect, because some storage mechanism must exist so that species can persist from one year to the next. Adondakis and Venable (2004) found that under a particular set of field conditions, one species may produce more seedlings in a given year than another and vice versa. Moreover, species differ in the environmental conditions under which each does best, which is also affected in some cases by the environmental conditions in the previous summer.

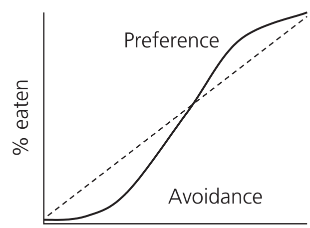

Fig. 5.1 Mechanism of lottery model of coexistence. Following this model, there should be avoidance of species when rare and they should be preferred when common.

Source: After Stiling (2002). With kind permission of Prentice-Hall.

5.1.2 Interactions among desert shrubs

Many studies have inferred the presence of interspecific shrub–shrub competition by means of nearest-neighbour distances (e.g. Phillips and MacMahon 1981; Briones et al. 1996; Carrick 2003; Wiegand et al. 2006). That is, if shrubs are considered to be competing with one another they should be very evenly dispersed (called 'overdispersed'), while if they are not competing they may have either a random or a contagious (clumped) distribution (Wiegand et al. 2006). In the latter case, facilitation may occur where there is a positive effect of one species' presence on that of another.

The nearest-neighbour technique was used by Carrick (2003) in the arid Karoo of South Africa. He found evidence for both intraspecific and interspecific competition among two Mesembryanthema species (*Ruschia robusta* and *Leipoldtia schultzei*) and a member of the Asteraceae (*Hirpicium alienatum*). Neither of the two Mesembryanthema species dominated *Hirpicium* although *Leipoldtia* was dominant over *Ruschia*. The two Mesembryanthema species had most of their roots in the top 5 cm of soil, whereas the asteraceous shrub had most of its roots at greater depths. This rooting niche separation may have led to the lack of effect on *Hirpicium* and the strong negative effect of *Leipoldtia* on *Ruschia*. Both of the Mesembryanthema species can use small-pulsed rain events but presumably, where the species grow in close proximity, *Ruschia* must suffer the negative effects of competition with *Leipoldtia*.

An experimental study was used by Schleicher et al. (2011a) in the arid Northern Cape province of South Africa. They found that when *Acacia mellifera* was removed from ten 1-ha plots, there was more recruitment of juvenile *Tarchonanthus camphoratus* and that plants of this latter species grew larger in the absence of competition from *Acacia mellifera* (Fig. 5.2). They also found that *Acacia mellifera* was positively associated with *Tarchonanthus camphoratus* (Asteraceae) when the latter species was a juvenile (facilitation) but negatively associated when both species were adults (competition).

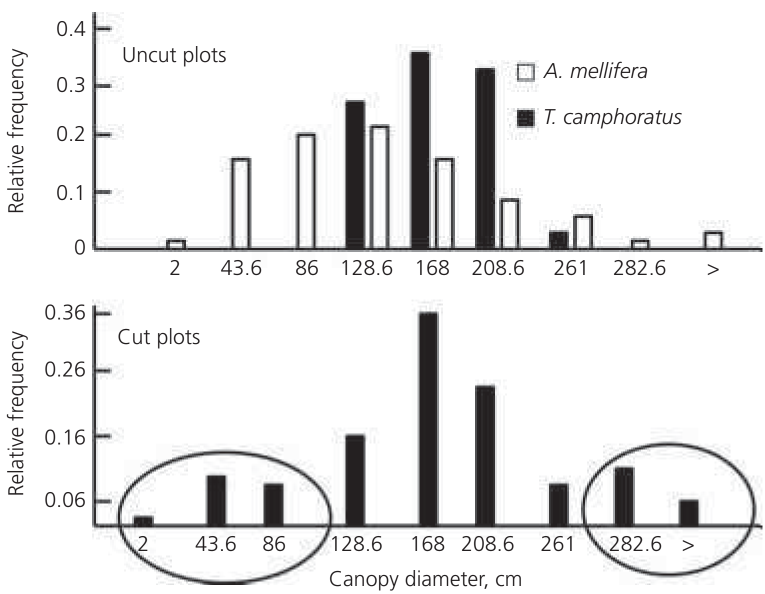

Fig. 5.2 Schleicher et al. (2011a) found that *Tarchonanthus camphoratus* (Asteraceae) in the arid Northern Cape can shift ontogenetically from being facilitated by growing close to adult *Acacia mellifera* (Fabaceae) early in life to competition with the adults as they age. Note the difference in size distributions in the plots from which *Acacia mellifera* was removed—there were more juvenile *Tarchonanthus camphoratus* and the adult *Tarchonanthus camphoratus* grew larger when *Acacia mellifera* was removed (circles).

Source: From Schleicher et al. (2011a). With kind permission of Elsevier.

Tielbörger and Prasse (2009) examined the effect of timing of seedling emergence, which may have a strong effect on fitness in competitive environments. They examined the germination fraction and time to germination in four coexisting perennial species (*Stipagrostis scoparia* (Poaceae), *Moltkiopsis ciliata* (Boraginaceae), *Cornulaca monacantha* (Chenopodiaceae), and *Artemisia monosperma* (Asteraceae)) in the sand dunes of the Negev Desert. They ran an experiment with low and high seed densities in intraspecific and interspecific neighbourhoods, with and without newly emerged seedlings. They found that neighbours accelerated germination independent of density. This pattern appeared to be caused by the presence of newly emerged seedlings. They found that germination fractions (but not rate of germination) were lower when seed densities were high. What was quite fascinating was that this effect of high density occurred even when neighbours did not germinate, suggesting that seeds were able to sense each other prior to emergence! Early germination may be adaptive because fast-emerging seedlings may gain a competitive advantage over slower ones.

5.1.3 Fairy circles, heuweltjies, and mima mounds—competition, herbivory, or self-organization?

There is considerable fascination about the origin of repeated circular and linear vegetation structures in arid regions. Circular vegetation is particularly dominant in the arid areas of the Karoo in South Africa (where they are called 'heuweltjies' or little hills) and in the arid parts of the Namib Desert in Namibia and Angola (where they are called 'fairy circles'). Circular vegetation is also present in certain deserts in South and North America, where they are known as mima mounds or nabkhas. Additional circular vegetation patterns occur in North America that are not in mima mounds (Ravi et al. 2008). These circular vegetation patterns are clearly overdispersed, indicating that some form of competition is occurring (Getzin et al. 2015).

5.1.3.1 Fairy circles

Either the area in the centre of the ring consists of bare soil, with the ring being formed often by a single grass species (fairy circles), or the vegetation on the inside of the ring is different from the ring itself (heuweltjies and mima mounds). In some cases, the circular vegetation patterns in fairy rings in Namibia are reported to result from intraspecific competition of the grass species (*Stipagrostis* species mostly) that predominate in them (Cramer and Barger 2013), in much the same fashion as the fungal hyphae that led to the creation of the term 'fairy ring'. Danin and Orshan (1995) noted that the growth of the horizontal rhizome of *Stipagrostis ciliata*, a common species of fairy circles in both the Namib and Negev deserts, would naturally result in the formation of fairy circles over time. A similar pattern of growth occurs in the Australian spinifex species *Triodia* (Nano and Clarke 2008), leading to a variegated vegetation pattern. Ravi et al. (2008) made a similar argument with respect to *Bouteloua gracilis* grass rings in the northern Chihuahuan Desert. They found that ring patterns result from the interaction between clonal-growth mechanisms and abiotic factors such as hydrological (specifically, water infiltration) and aeolian processes. These processes result in a negative feedback between sediment deposition and vegetation growth inside the bunch grass, which leads to grass dieback at the centre of the grass clump. Soriano et al. (1994) found that grasses grew around certain shrub species (*Senecio filaginoides, Mulinum spinosum*, and *Adesmia campestris*) in the arid Patagonian shrub steppe, resulting in a circular pattern. They believed that this was largely due to facilitation, presumably caused by improved environmental conditions, such as greater water availability.

Albrecht et al. (2001) suggested that there was some as yet unknown allelopathic substance in the bare soils in the centre of these fairy-circle rings. Jankowitz et al. (2008) and Naudé et al. (2011) found evidence for geochemical hydrocarbon microseeps that might explain fairy circles. However, Cramer and Barger (2013) note that these geochemical substances can't explain the overdispersed (competitive) spatial patterning (Getzin et al. 2015) (Fig. 5.3). Furthermore, dead vegetation and grass residues, such as occur in the centre of the rings, may also alter hydrocarbon concentrations. Meyer et al. (2015) found evidence of triterpenoids (a chemical defence compound) from *Euphorbia damarana* in the southern Namib Desert in the centres of fairy circles. This was very similar to the claim by Theron (1979) in the northern Namib (Kaokoland) that *Euphorbia damarana* was the cause of fairy circles. Here

Fig. 5.3 This aerial image of fairy circles in the Marienfluss in northern Namibia shows that there are positive short-distance feedbacks of vegetation growth, leading to additional biomass accumulation around fairy circles while eco-hydrological feedbacks cause water depletion at larger distances away from the circles. In agreement with vegetation self-organization, this spatial gradient in water availability will lead to the emergence of new fairy circles in-between older ones.

Source: From Getzin et al. (2015). Image: Stefan Getzin.

too it would be difficult to explain overdispersion (*sensu* Cramer and Barger 2013). However, if *Euphorbia damarana* plants were competing with each other, overdispersion would be expected. Other scientists have suggested that it is herbivory by termites (Lovegrove and Siegfried 1986, 1989; Becker and Getzin 2000; Grube 2002; Van Rooyen et al. 2004; Jürgens 2013, 2015) or ants (Picker et al. 2012) that leads to differential growth of the grass species. In the case of the Namibian fairy circles, a single grass species (either *Stipagrostis giessii* or *Stipagrostis ciliata*) predominates in the ring of peripheral vegetation, with *Stipagrostis obtusa* and *Stipagrostis uniplumis* in the surrounding grassland matrix (Cramer and Barger 2013).

Another, more plausible idea is that it is self-organization that maintains them (Fernandez-Oto et al. 2013; Getzin et al. 2015). At this stage, it appears that competition of grass for water together with positive biomass-water feedbacks involving water transport towards growing vegetation patches results in self-organized vegetation patterns (Cramer and Barger 2013; Getzin et al. 2015). Zelnik et al. (2015) note that only self-organized biomass-water feedbacks can explain the shrinking in size and disappearance of fairy circles after above-average rainfall years and the typical enlargement and increased appearance of fairy circles after below-average rainfall years. While the presence of termites and/or ants may be consistent with the existence of fairy circles (Picker et al. 2012; Jürgens 2015), it is unlikely that they are the reason for fairy-circle creation. Getzin et al. (2015) have also indicated that tiger bush (i.e. the presence of stripes of perennial vegetation) that commonly occurs in the arid Sahel region of central-west Africa is also likely to be due to self-organization due to competition of bush for water linked to positive biomass-water feedbacks (see also Lefever and Lejeune 1997; Klausmeier 1999; Von Hardenberg et al. 2010). Getzin et al. (2016) have also found a fairy-circle system in arid Western Australia where there is no connection to the distribution of termites (or ants). They found that these patterns emerge by self-organization. The mechanism in Australia is a positive biomass-water feedback associated with water runoff and biomass-dependent infiltration rates (Fig. 5.4). Rainfall events in this arid area cause excess rain to flow as runoff water over the gap surface towards the vegetation matrix. The runoff is induced because of the sharp infiltration contrast between the gaps and the matrix which makes the rain-hardened gaps an important additional source of water for the vegetation matrix. While supporting the spinifex (*Triodia basedowii*) grasses at the periphery and the matrix, the overland-water flow acts against seedling establishment and growth in the gaps by reducing the amount of infiltrated water. Additionally, the hard soil crust in the gap causes plant death because root growth is hampered and high soil-surface temperatures and the associated high evaporation rates provide a hostile micro-environment for plant survival. In contrast, the shading within the vegetation matrix and its periphery reduces surface temperatures by more than 20°C and thus the evaporation rates, and thereby further facilitates grass growth. The similarity between the patterns of Australian and Namibian fairy circles supports a central principle of pattern-formation theory and the applicability of this theory to wider contexts of spatial self-organization in ecology.

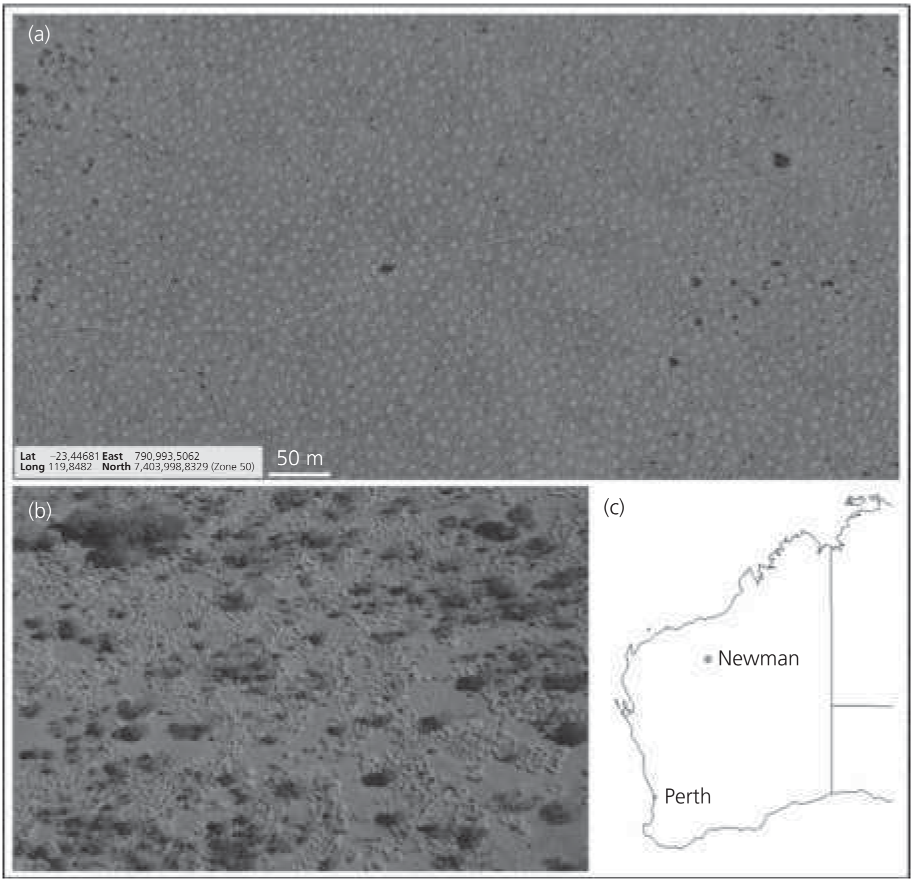

Fig. 5.4 The fairy circles of Western Australia. Aerial image of the regularly spaced gaps (a). Self-organized formation of the gap pattern within spinifex (*Triodia basedowii*) grasses under spatially various proportions of bare soil (b). Map of Western Australia (c), where the fairy circles can be found to the east and south of the town Newman.

Source: From Getzin et al. (2016). Permission of Stephan Getzin.

5.1.3.2 Heuweltjies

It appears that the formation of heuweltjies differs from that of fairy circles. Heuweltjies are often more woody than the surrounding areas, but in some cases may have more succulent plants or be more grassy than in the surrounding vegetation. The key factor is that they too are circular and appear to result from competition (Cramer and Midgley 2015). While it has been considered that termites (and perhaps burrowing mammals) were also responsible for the creation of heuweltjies (Lovegrove and Siegfried 1986, 1989) by redistribution of mound materials, it appears that this too may be a case of confusing cause and effect. Colonies of the termite

Microhodotermes viator are indeed frequently associated with heuweltjies but these create nutrient-rich islands, which affect the amount of vegetation on the mound but not the presence of the mound per se (McAuliffe et al. 2014). McAuliffe et al. (2014) propose that the well-sorted, fine to very fine sands that constitute the bulk of the mounds (mound diameters range from 9 to 42 m) are aeolian sediments, deposited within localized zones of greater vegetation density associated with termitaria of the *Microhodotermes viator*. Within sparsely vegetated arid and semi-arid regions, slight differences in vegetation cover promote local accumulation of aeolian sediments. Some examples of variation in vegetation cover include the development of coppice dunes (coppice mounds) or 'nabkhas' associated with the windbreak effect of woody plants (Langford 2000; McAuliffe et al. 2007). Accumulation of windborne sediments beneath denser vegetation associated with heuweltjies is similar with one important exception—the remarkably regular spacing of heuweltjies. Here, termites may play an important role. McAuliffe et al. (2014) explained this overdispersion as being a consequence of territorial interactions between members of neighbouring termite colonies (Laurie 2002). *Microhodotermes viator* have been observed feeding up to 45 m from the central nest (Coaton and Sheasby 1974) and spacing between neighbouring heuweltjies is typically on the order of 50–75 m (McAuliffe et al. 2014). However, more recently, Cramer and Midgley (2015) have suggested that termites may not be responsible for this regular spacing. They found that overdispersion was strongest and the sizes of the mounds smallest when these mounds were close to one another. Cramer and Midgley (2015) have shown that mean annual wind velocities in areas where heuweltjies are common are typically quite high. They inferred that mounds that were close to one another were competing for aeolian sediment accretion.

Investigators have variably attributed nabkhas in North America to earth-moving activities of fossorial mammals (Cox and Allen 1987; Howath and Johnson 2006), spatially variable vegetation, and associated differences in either sediment deposition or soil erosion (Siefert et al. 2009; Weems and Monger 2012), as well as non-biotic factors (Siefert et al. 2009; Zaitlin and Hayashi 2012). However, Siefert et al. (2009) provided evidence that mounds from multiple sites in North America represent relict nabkhas that originally formed when extended, long-term droughts reduced vegetation cover, leading to accumulation of aeolian sediments beneath patches of remaining vegetation cover. Thus, it appears that self-organization is a likely cause of fairy rings but aeolian sediment accretion may be the cause of heuweltjies. Soil erosion may be the cause of mima mound or nabkha formation, but perhaps the jury is still out on this issue?

5.1.4 Facilitation and nurse-plant effects

A great number of shrubs have been shown to have nurse-plant effects on annual plants in particular, although other shrubs and geophytes (see Fig. 5.5) may also benefit from this (see review by Callaway 1995). Essentially, this means that the annual plants grow up under the shrub and benefit from a number of factors. These factors include increased water availability (including from hydraulic lift—see Chapter 3),

Fig. 5.5 *Sternbergia clusiana* (Amaryllidaceae) benefiting from facilitation by the thorny *Sarcopoterium spinosum*.

lower soil temperatures created by shading, and higher resource availability, particularly higher nitrogen availability. For example, Franco and Nobel (1989) found that complete shading from direct sunlight decreases maximum soil surface temperatures in summer by 11°C, which also had strong effects on the internal temperatures of the cacti *Carnegiea gigantea* and *Stenocereus thurberi*. Desert legumes, in particular, can alter the availability of soil nitrogen (Kambatuku et al. 2013b). Columnar cacti established beneath trees or shrubs may ultimately outcompete the nurse plants, leading to a cyclical succession process (Yeaton 1978; McAuliffe 1988), where sun-tolerant shrubs colonize open spaces, providing shade (and other factors just mentioned) to another set of colonists and, in the end, are outcompeted by these other plants (Suzán et al. 1996; Tielbörger and Kadmon 2000).

Osem et al. (2004, 2007) found that the spiny shrub *Sarcopoterium spinosum* (Rosaceae) in the northern Negev Desert (Israel) has significant facilitative effects on annual plants growing under them that depend on the presence of grazing and topography. On north-facing slopes, where there is grazing, facilitative effects occur (Osem et al. 2007), especially for large annuals and some geophytes (Fig. 5.5). There was no effect on south-facing slopes (Osem et al. 2007).

Schleicher et al. (2011b) examined the interactions between *Acacia erioloba* (Fabaceae) and *Grewia flava* (Rosaceae), an arid area of northwestern South Africa. They found that there was no evidence of a negative interaction between these two species. In fact, there was a positive interaction, indicative of facilitation or, perhaps, differential seed dispersal under the host trees. In the case of the latter, *Grewia flava* has relatively large fruits that are consumed by birds while *Acacia erioloba* can be a large tree. Frugivorous birds sitting in *Acacia erioloba* trees could defecate seeds of *Grewia flava*, resulting in a positive association between these two species. Facilitation could occur because of the considerable root depths of *Acacia erioloba*, resulting in hydraulic lift from the tree benefitting *Grewia flava*. *Acacia erioloba* is also a legume, which may also benefit *Grewia flava* by means of nitrogen fixation.

Sotomayor et al. (2014) studied the seeds of five desert annual species (*Alonsoa meridionalis, Cyperus hermaphroditus, Fuertesimalva peruviana, Nassella mucronata*, and *Plantago limensis*) under the nurse plant *Caesalpinia spinosa* from the Atiquipa coastal desert in southern Peru. They compared their growth under the canopy of *Caesalpinia spinosa* to open areas between these plants. They predicted that seeds collected from under the nurse-plant canopy would be (i) larger due to more favourable growing conditions, (ii) more viable and have greater germination rates, (iii) less variable in size and viability due to reduced environmental heterogeneity, and (iv) able to germinate faster to avoid apparent competition with other annuals. They found that only two (*Cyperus hermaphroditus* and *Nassella mucronata*) of the five species were strongly facilitated by the nurse plant. They measured this by means of an index known as the Relative Interaction Intensity (RII) using plant density, where RII = (density under canopy – density in the open)/(sum of the densities). One of the five species (*Plantago limensis*) had a neutral response in RII. Two of the species were inhibited in their densities when under the canopy of the nurse plant (*Alonsoa meridionalis, Fuertesimalva peruviana*) (Fig. 5.6). They found no significant differences in seed mass, viability, or relative variability between understory and open microhabitats for any of the species. Final germination rates of seeds from open microhabitats were higher than under the canopy of the nurse plants, and the open microhabitat was more favourable for germination

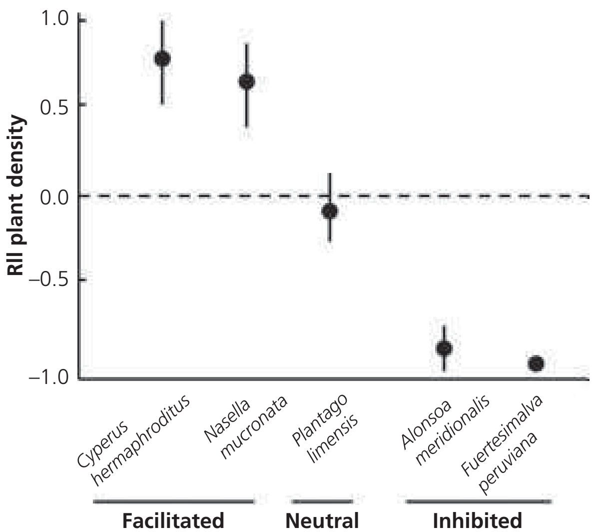

Fig. 5.6 Relative interaction intensity (RII) indices for plant density of five annual plant species growing in open and understory microhabitats in Atiquipa, southern Peru.

Source: From Sotomayor et al. (2014). With kind permission of John Wiley and Sons.

of the seeds of these annual species. Thus, these results do not provide supportive evidence of facilitation in seed traits.

A number of factors affect the spatial distribution of nutrients in desert ecosystems. Most importantly, perhaps, is the effect of so-called 'islands of fertility', where individual shrubs, or occasionally trees, create unique microhabitats for other plants to grow under (Ravi et al. 2010). Note that facilitative effects do not always occur (Tielbörger and Kadmon 2000).

An interesting relationship occurs when there is a cyclical relationship between plant species, such as between mesembryanthemaceous and succulent species and woody plants in the Karoo Desert in South Africa (Yeaton and Esler 1990; Adie and Yeaton 2013). Adie and Yeaton (2013) found, in an arid area of subtropical thicket (also known as arid thicket; Vlok et al. 2003) near Jansenville in the Eastern Cape, South Africa, that *Portulacaria afra* (an arborescent succulent shrub) was responsible for important nutrient cycling processes and was important in the facilitated recruitment of tree seedlings. Vlok et al. (2003) proposed that *Portulacaria afra* may facilitate recruitment of thicket species. Heavy grazing by livestock has caused extensive transformation of the thicket to a more savanna-like vegetation that consists of scattered trees, ephemeral plants, and dwarf shrubs (Lechmere-Oertel et al. 2005, 2008). About 90% of the fleshy-fruited tree seedlings were recorded under *Portulacaria afra* clumps (mostly due to vertebrate dispersal; Adie and Yeaton 2014) and 93% of *Portulacaria afra* seedlings, dispersed there by the harvester ant *Messor capensis* (Adie and Yeaton 2014), were recorded under woody shrubs (especially *Rhigozum obovatum*). The growth of the *Portulacaria afra* clump leads to a decline in the canopy cover of *Rhigozum obovatum*. Stems of *Rhigozum obovatum* can collapse as the *Portulacaria afra* clump increases in height. Four lines of evidence were used to support the hypothesis that canopy tree establishment is facilitated by *Portulacaria afra*:

(1) Seedlings of all canopy trees (except *Gymnosporia polyacantha*) were recorded only from *Portulacaria afra* clumps and never from open microsites.
(2) Most adult trees were found in *Portulacaria afra* clumps and were generally associated with nutrient-rich patches under these *Portulacaria afra* clumps.
(3) Mature trees such as *Grewia robusta* and *Lycium oxycarpum* were found more frequently on the shady side of *Portulacaria afra* plants, which is consistent with the importance of shade in facilitating trees and woody shrubs in arid environments (Maestre et al. 2003).
(4) The relative shade intolerance of canopy trees retards their growth once established (Holmes and Cowling 1993), causing them to grow to the sunny side of the *Portulacaria afra* clump.

However, Adie and Yeaton (2013) recognize that there is a severe recruitment bottleneck, limiting the establishment of these woody trees to events of high and sustained rainfall (Wiegand et al. 2005). They also recognize that herbivory has a major role to play in arid environments (Graff et al. 2007). Unlike woody and thorny shrubs such as *Rhigozum obovatum*, the succulent *Portulacaria afra* offers little protection from herbivory, indicating that it is herbivory rather than rainfall that is of key importance in this particular area. *Lycium cinereum*, a woody shrub, and the stem-succulent *Psilocaulon absimile* were found more frequently on nutrient-rich patches than expected by chance alone. Both *Lycium cinereum* and *Psilocaulon absimile* were replaced by grasses (especially *Aristida congesta*) as the nutrient-rich patch got older. Although grasses tend to outcompete woody shrubs (e.g. Kraaij and Ward 2006; Tjelele et al. 2015), they may also may ameliorate germination conditions. Grass may offer regeneration conditions for the woody shrub *Rhigozum obovatum*. In turn, *Rhigozum obovatum* offers improved germination conditions for the succulent *Portulacaria afra*, which in turn offers improved conditions for tree establishment (Fig. 5.7). Adie and Yeaton (2013) show that plant species replacement patterns were facilitated by nurse plants, resulting in a predictable sequence of species replacement that is cyclical (also called non-successional dynamics; Verdu et al. 2009).

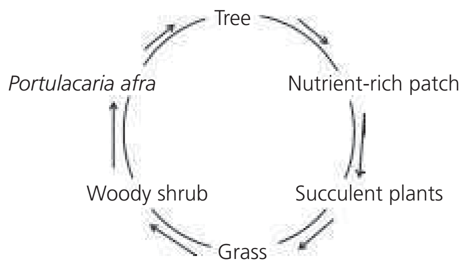

Fig. 5.7 Cyclic succession among *Portulacaria afra*, succulent plants, grass, and trees.
Source: From Adie and Yeaton (2013). With kind permission of Elsevier.

An important effect comes from a variety of animal species. The term now used for these physical effects of animals on ecosystems is *ecosystem engineering* (Jones et al. 1994). In deserts worldwide, termites play an important role, perhaps more than any other organism, largely because of their effects on decomposition (Whitford 2002; see Chapter 10), but also because they produce macropores that allow the infiltration of water into the soil to depths of as much as 2 m (Whitford 2002). Harvester ants have large effects on ecosystems because they collect seeds from considerable distances and disperse them close to their mounds, where they later germinate. Wilby et al. (2001, 2005) have shown that the harvester ant *Messor ebeninus* had a particularly large effect on the crucifer *Reboudia pinnata*, which increased in abundance from about 10% of samples on undisturbed soil to about 85% of samples on mound samples. The terminal seeds in each pod of *Reboudia pinnata* are surrounded by a hardened fruit wall, which protects the seeds from predation (Gutterman 1993). A total of 55 species were found on the nest mounds of harvester ants compared with 25 on undisturbed soil (Wilby et al. 2001).

5.2 Competition between animals

MacArthur and Pianka (1966), Rosenzweig (1985), and Brown (1988) and others have developed theories regarding the role of competition in arid areas that work at different scales, specifically the patch scale (Brown 1988) and the habitat scale (MacArthur and Pianka 1966; Rosenzweig 1985; Wasserberg et al. 2007).

5.2.1 Patch scale

Brown's (1988) model considers how animals make decisions regarding which patch to stay in and for how long. Animals must make decisions to stay in a patch based on the combined effects of competition, predation risk, and the missed opportunity costs of not foraging elsewhere. Predation risk also affects patch selection because the perceived risk of being eaten is probably as important (or even more so) as actually being consumed. For example, predators that are prevented from killing their prey can separate non-lethal predation behaviour from direct mortality effects. Ford et al. (2014) and Laundré et al. (2014) have shown that non-lethal behavioural predation effects (predation risk) can be a significant component of competitive effects (see Chapter 6). Missed opportunity costs (MOC) is a term borrowed from microeconomic theory and considers that, when one makes a decision to do something, one is not only considering the value of that alone but also its value relative to something else one is not doing at the time—this is MOC. For example, one buys an item with the limited money one has, there is a missed opportunity to buy something else. Brown (1988) considered the optimal use of a patch. This is when the patch harvest rate (H) is no longer greater than the sum of the energetic (C), predation (P), and MOC of not foraging elsewhere. Thus, an animal forages in a patch or habitat until

$$H = C + P + \text{MOC}$$

Brown (1988) also developed the practical technique of assessing giving-up densities (GUDs) to demonstrate this. Basically, an amount of seed is placed in a tray with a large amount of the substrate to mimic the natural foraging conditions experienced by an animal. In many cases, a constant amount of millet is placed in sand to mimic the natural foraging conditions for desert rodents (Hughes and Ward 1993; Ziv et al. 1993, 1995; Hughes et al. 1994). The more seed removed from the tray, the greater the perceived value of the tray and vice versa. Conversely, if a tray has low perceived value (i.e. H (the harvest rate) is low relative to C (energetic costs of foraging) or P (predation risk) or MOC (missed opportunity costs of not foraging elsewhere)), then it should have a high GUD and the animal moves on to the next patch.

Some of the most exciting research on patch use has involved desert granivores. In the Negev Desert (Israel), Ziv et al. (1993) examined the factors that affect competition between two gerbil species. The larger species, *Gerbillus pyramidum* (mean mass = 40 g), dominates in the semistabilized dunes of the western Negev while the smaller species, *Gerbillus andersoni allenbyi* (mean mass = 26 g), prefers the same habitat but is often forced to occupy a secondary habitat of stabilized dunes. This system was shown to be one of shared-preference habitat selection by Abramsky et al. (1990). Ziv et al. (1995) showed that the higher sand content of the semistabilized sands made it more efficient for both species to forage there. Ziv et al. (1993) found that *Gerbillus pyramidum* was active in the early evening (until about 22h00) and *Gerbillus andersoni allenbyi* in the later part of the night. Ziv et al. (1993) suspected that interference competition was responsible; that is, *Gerbillus pyramidum* was competitively excluding *Gerbillus andersoni allenbyi* by interference. They demonstrated, by the exclusion of *Gerbillus pyramidum* from some plots, that this was indeed the case (Fig. 5.8). For the earlier-mentioned mechanism to work, seeds need to be replaced within the same evening. Ben-Natan et al. (2004) found that sufficient seeds were available for *Gerbillus andersoni allenbyi* to use in the second part of the night (Fig. 5.9).

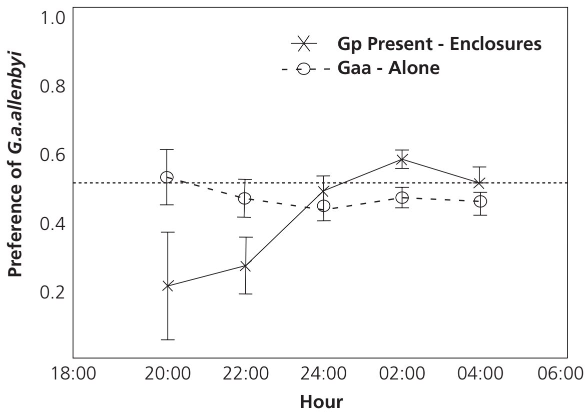

Fig. 5.8 Ziv et al. (1993) excluded *Gerbillus pyramidum* from plots also containing *Gerbillus andersoni allenbyi*. They found that *Gerbillus pyramidum* was engaged in interference competition with *Gerbillus andersoni allenbyi*. Where *Gerbillus pyramidum* occurred with *Gerbillus andersoni allenbyi*, the latter species avoided these areas in the early evening and preferred the plots later in the night. This indicated that *Gerbillus pyramidum* was temporally excluding *Gerbillus andersoni allenbyi* from being active in the early evening.

Source: From Ziv et al. (1993). With kind permission of Blackwell.

5.2.2 Habitat selection models

Rosenzweig (1991) differentiated between distinct and shared preference models of habitat selection, both of which assume that habitat selection is density-dependent. Distinct preference models indicate that different habitats are preferred by each species while shared preferences indicate the preferences are the same. A particular type of shared preference is centrifugal community organization (Rosenzweig and Abramsky 1986). In this form of habitat selection, the same (core) habitat is preferred but each species has a different secondary habitat in which they are dominant (see also Ward and Seely 1996b). Stable coexistence

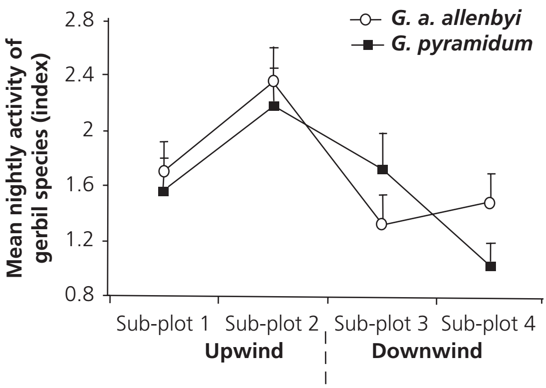

Fig. 5.9 Ben-Natan et al. (2004) found that seeds need to be replaced within the same evening for temporal partitioning to work as a mechanism of coexistence so that sufficient seeds could be available for *Gerbillus andersoni allenbyi* to use in the second part of the night. They used fences placed in a semicircle on semistabilized dunes. Subplot 1 was 1.6 m upwind of the fence, subplot 2 was immediately upwind (and against) the fence, subplot 3 was immediately downwind (and against) the fence, and subplot 4 was 1.6 m downwind of the fence. The results show that the activity (range = 0.4) of *Gerbillus pyramidum* was lower than *Gerbillus andersoni allenbyi* on the downwind side of the fence only.

Source: From Ben-Natan et al. (2004). With kind permission of Blackwell.

can only be achieved when the species have different secondary habitats in which they are dominant (Rosenzweig and Abramsky 1986). It is assumed that density-dependent habitat selection is based on exploitation competition, i.e. that one species exploits the food resources at a greater rate than the other species. Wasserberg et al. (2007) tested the centrifugal community organization model on *Gerbillus pyramidum* and *Gerbillus andersoni allenbyi* in the Negev Desert. These two species occurred on three sand-dune types: shifting, semi-stabilized, and stabilized dunes. They found that both *Gerbillus pyramidum* and *Gerbillus andersoni allenbyi* did best on a single dune type, the semi-stabilized dune, which is consistent with the centrifugal model. Also consistent with the centrifugal model, they preferred different secondary habitats. *Gerbillus pyramidum* preferred the shifting dunes and *Gerbillus andersoni allenbyi* preferred the stabilized dune. Furthermore, habitat selection was density-dependent, a third key factor in the centrifugal model. However, in contrast to the centrifugal model, they found that *Gerbillus pyramidum* preferred the core (semi-stabilized dune) habitat and excluded *Gerbillus andersoni allenbyi*. Wasserberg et al. (2007) believe that the general tenets of Rosenzweig and Abramsky's (1986) centrifugal community organization model were supported but differed in the sense that the dominance of one species over the other made it what they termed 'asymmetric centrifugal community organization'. They believe that interference competition (rather than exploitation competition) by *Gerbillus pyramidum* on *Gerbillus andersoni allenbyi* led to the asymmetry that they observed.

5.3 Indirect interactions: keystone species and apparent competition

A useful example for demonstrating the difference between indirect and direct effects comes from the Chihuahuan Desert of North America, which occurs via the indirect effects of rodents on ants that are mediated via effects on annual plants. Davidson et al. (1985) found that ants increased in density and then decreased after rodent removal (Fig. 5.10). For the first 2 years, densities of ant colonies were twice as high on rodent removal plots as on control plots. By the 3rd year, ant colonies were nearly equally dense on control and removal plots. From the 4th year on, ant colony densities declined, nearing extinction by the 11th year. The ant response to rodent removal was an indirect and not a direct increase because rodents eat larger seeds than ants do, and large-seeded plants compete with smaller-seeded plants. Any initial advantage to the ants of rodent removal was lost when the large-seeded plants outcompeted the smaller-seeded plants. Rodents indirectly benefited ants by controlling the increase of competitively superior large-seeded plants.

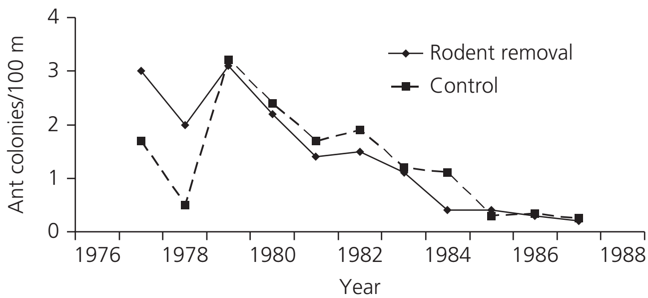

Fig. 5.10 Davidson et al. (1985) found that ants increased in density and then decreased after rodent removal.

Source: From Davidson et al. (1985). With kind permission of the Ecological Society of America.

5.3.1 Keystone species

A dominant species has effects that depend on biomass or numbers and are proportional to those effects. However, a keystone species has effects that are considerably greater than simple dominance (Paine 1966). For example, Munzbergova and Ward (2002) showed that *Acacia raddiana* trees (Fabaceae) are keystone species in the Negev Desert (Israel) (Fig. 5.11). In populations with high *Acacia* mortality, an average of five other plant species disappear. They also showed that plant species diversity is higher under trees than in the open spaces between trees. In this sense, *Acacia* trees act like nurse plants, increasing diversity (Fig. 5.11). However, they differ from nurse plants in that it is the species itself that is important. Once that species disappears from the ecosystem, it is not replaced by other species with similar

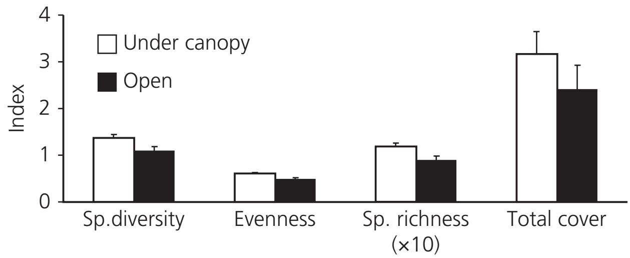

Fig. 5.11 Munzbergova and Ward (2002) showed that plant species diversity is higher under *Acacia raddiana* trees than in the open spaces between trees.

Source: From Munzbergova and Ward (2002). With kind permission of Opulus Press.

effects. One of the most important effects of *Acacia* species on the soils was through increased nitrogen, which in turn benefited the plants growing under the trees (see also De Boever et al. (2015) for an example of the positive effects on the soil of the same species growing in Tunisia). This *Acacia* species, similar to many others, fixes nitrogen. *Acacia* trees are also capable of hydraulic lift, which will benefit many shallow-rooted species occurring in their vicinity. Similar keystone effects have been demonstrated for *Acacia erioloba* (Milton and Dean 1995) and by Suzán et al. (1996) for *Olneya tesota* (both Fabaceae).

5.3.2 Short-term apparent competition

Holt and Kotler (1987) considered the situation where two prey species are consumed by a third predator species. They assumed that neither of the prey species competes with the other, but that more predators persist when both prey species are present because more total food is available for the predator. The net result is that there should be more predation when both are present. Thus, each prey species has a negative indirect effect on the other through its direct positive effect on the abundance of the predator (Fig. 5.12). Veech (2001) tested for apparent competition by examining the foraging behaviour of two heteromyid rodent species (Heteromyidae, Rodentia), Merriam's kangaroo rats (*Dipodomys merriami*) and little pocket mice (*Perognathus longimembris*). Veech (2001) tested the preferences of both rodent species for the seeds of eight plant species. Both rodent species exhibited distinct but

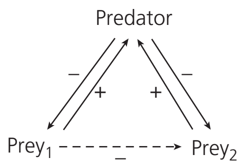

Fig. 5.12 Short-term apparent competition. Solid line: direct effect; dashed line: indirect effect.

variable preferences for some seeds and avoidance of others. However, the differences in preference appeared to have only an occasional effect on the strength of the short-term apparent competition detected in a field experiment. Veech (2001) found that captive individuals of both rodent species had approximately equal foraging effort (i.e. time spent foraging) in patches that contained a highly preferred seed type (*Oryzopsis hymenoides*) regardless of seed density and the presence of a less preferred seed type (*Astragalus cicer*) in the patches. The rodents also harvested a large proportion of *Oryzopsis hymenoides* seeds regardless of initial seed density; this precluded a negative indirect effect of *Astragalus cicer* on *Oryzopsis hymenoides*. However, there was a negative indirect effect of *Oryzopsis hymenoides* on *Astragalus cicer* caused by rodents having a lower foraging effort in patches that only contained *Astragalus cicer* seeds than in patches that contained *Astragalus cicer* and *Oryzopsis hymenoides* seeds. The indirect interaction between *Oryzopsis hymenoides* and *Astragalus cicer* represented a case of short-term apparent competition that was non-reciprocal. Most importantly, this indirect interaction was caused by the foraging behaviour of the rodents.

6 The Importance of Predation and Parasitism

A number of excellent experimental studies have demonstrated the importance of predation in structuring desert ecosystems, and how predation and competition interact to structure desert communities. There are two ways that predation can be effective: (1) by direct mortality (Abramsky et al. 1990, 1992; Hermony et al. 1992); and (2) by the predation risk experienced by the animal (Kotler et al. 2004).

6.1 Direct mortality

As an example of direct mortality, Abramsky et al. (1990, 1992) and Hermony et al. (1992) considered the effects of direct predation on desert snails by two species of desert rodents, *Gerbillus dasyurus* and *Acomys cahirinus*. In the central Negev Desert highlands of Israel, rodents forage on the rocky hillsides of the wadi–hillslope ecosystem (see Fig. 2.9). The rodents are primarily found on the upper slopes where there are burrows available. They consume their snail prey (mostly *Trochoidea seetzenii*) and deposit them in piles, colloquially known as 'feeding tables'. Abramsky et al. (1990) made use of artificial shelters for rodents because they found that natural shelters were a limiting factor for the rodents. They found that rodent densities increased in areas with artificial shelters and that snail densities decreased. They found that there was a direct negative effect of predation by the rodents on snail numbers and that there was an indirect effect induced by the movement of the snails from the wadis to the hillsides. Hermony et al. (1992) showed that snails primarily bred in wadis during the winter rains (as found by Ward and Slotow 1992) and moved on to the lower slopes in the summer months. The rodents are restricted in their movements by their own predators (such as owls and foxes) to the upper hillslopes. Thus, the rodent–snail interaction is maintained by spatial heterogeneity in the distributions of both snails and rodents, and by the sensitivity of rodents to predation risk by their own predators.

Groner and Ayal (2001) examined the effects of direct mortality of darkling or tenebrionid beetles (Tenebrionidae) by migratory birds on the size distributions of these beetles in the Negev Desert. Tenebrionid beetles in the Negev Desert exhibit size-related habitat segregation, with larger species found in denser cover and medium- and

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small-sized beetles found on the hillsides. Birds are purported to be the cause of size dependence in that plant cover reduces the predation efficiency of birds upon large tenebrionids, and birds prefer larger tenebrionids (especially *Adesmia dilatata* (spring active), *Trachyderma philistina*, and *Pimelia grandis* (the last two species are both summer active)). Groner and Ayal (2001) found that plant cover reduced predation rate by the most common spring and summer predatory birds, which were white storks (*Ciconia ciconia*) and stone curlews (*Burhinus oedicnemus*). Large tenebrionids are the most profitable size for a bird to consume, medium-sized species (e.g. *Adesmia metallica syriaca*) are less so (albeit still acceptable), and small species (e.g. *Opatroides punctulatus, Zophosis punctata, Adelostoma grande*) are unprofitable and are generally ignored. The well-vegetated wadi habitats are dominated by large and small species of beetles, whereas medium-sized tenebrionids are under-represented in this habitat. The results of cage experiments indicated possible apparent competition (see Chapter 5) between the large and the medium/small tenebrionids in the wadis. Groner and Ayal (2001) found that large (and profitable) species are refuge-dependent, as they need to hide under the bushes in the wadis. Storks had 79% lower predation rates when foraging in the highly vegetated wadis and stone curlews had 54% lower predation rates when foraging there. Medium-sized (acceptable) species use enemy-free space on the hillslopes (where there are no predators), and the distribution of the small species is essentially independent of avian predator activity.

Loria et al. (2008) studied the effects of predation by two types of predator on two types of antlion larvae (Myrmeleontidae). Antlion larvae are sand-dwelling insect predators, which ambush small arthropod prey while buried in the sand. In some species, the larvae construct conical pits and are considered as sit-and-wait predators which seldom relocate while in other antlion species, they ambush prey without a pit but change their ambush site much more frequently (i.e. sit-and-pursue predators). The ability of antlion larvae to evade some of their predators that hunt them on the sand surface is strongly constrained by the degree of sand stabilization or by sand depth. Loria et al. (2008) studied the effect of predator presence, predator type (active predatory carabid beetle, *Anthia sexmaculata* vs sit-and-pursue wolf spider (family Lycosidae), and sand depth (shallow vs deep sand) on the behavioural response of the pit building *Myrmeleon hyalinus* larvae and the sit-and-pursue *Lopezus fedtschenkoi* larvae. Predator presence had a negative effect on the activity of both antlion species. The sit-and-wait *Myrmeleon hyalinus* larvae showed reduced pit-building activity (Fig. 6.1), whereas the sit-and-pursue *Lopezus fedtschenkoi* larvae decreased relocation distances (Fig. 6.2). The proportion of relocating *Myrmeleon hyalinus* was negatively affected by sand depth, whereas *Lopezus fedtschenkoi* was negatively affected also by the predator type. Specifically, the proportion of individual *Lopezus fedtschenkoi* that relocated in deeper sand was lower when facing the active predator rather than the sit-and-pursue predator. The proportion of *Myrmeleon hyalinus* that constructed pits decreased in the presence of a predator, but this pattern was stronger when exposed to the active predator. The authors suggest that these differences between the two antlion species are strongly linked to their distinct foraging modes and to the foraging mode of their predators.

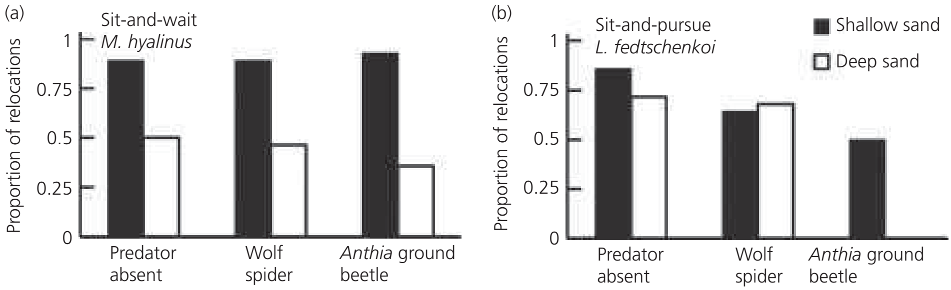

Fig. 6.1 The proportion of relocating *Myrmeleon hyalimus* (a) and *Lopezus feldtschenkoi* (b) antlion larvae in response to sand depth (deep and shallow) and the predator treatment (predator absent, active predatory beetle, or sit-and-pursue wolf spider present). *Myrmeleon hyalimus* is a sit-and-wait predator while *Lopezus feldtschenkoi* is a sit-and-pursue predator.

Source: After Loria et al. (2008). With kind permission of Springer.

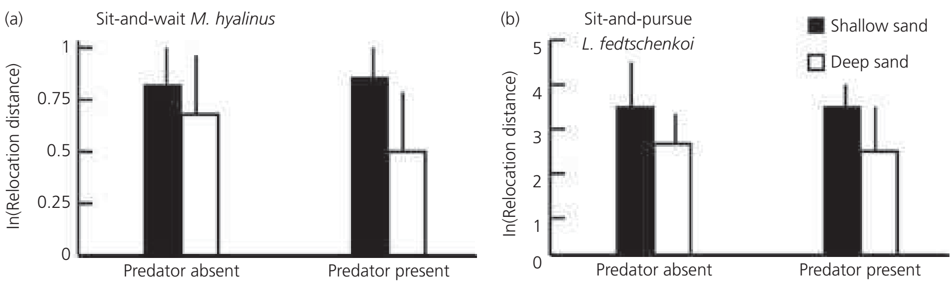

Fig. 6.2 The natural logarithm of the relocation distances of *Myrmeleon hyalimus* (a) and *Lopezus feldtschenkoi* (b) antlion larvae in response to sand depth (deep and shallow) and the predator presence. *Myrmeleon hyalimus* is a sit-and-wait predator while *Lopezus feldtschenkoi* is a sit-and-pursue predator. Mean ± S.D. values are represented.

Source: After Loria et al. (2008). With kind permission of Springer.

6.2 Predation risk

The effects of predation risk can have large consequences for patch use and habitat selection. For example, Kotler et al. (2004) consider apprehension, which is the behavioural change related to the risk of predation experienced by the animal that takes away from time available for foraging. Predation risk, which includes the time taken away from foraging and from direct observation of predators, should increase with energetic state of the animal (an animal that is in a higher energetic state should be able to spend more time in non-energy gaining activities). They tested the responses of Allenby's gerbil, *Gerbillus andersoni allenbyi* (Rodentia), in the Negev Desert

(Israel) to predation risk while altering the energetic state of the animal. They also altered the risk to the gerbils by introducing barn owls, *Tyto alba*. The gerbils took about 4.5 times more seeds when they were in a higher energetic state and took about 17% fewer seeds when barn owls were present. Seeds were presented when owls were present either in bush (sheltered) or in the open (i.e. unprotected) microhabitats; the gerbils took about 26% fewer seeds from the open microhabitats that were accessible to owls. Regarding time allocation, gerbils had higher giving-up densities (GUDs) (i.e. allocated less time foraging—see Chapter 5 for the explanation of GUDs) when the risk of owl predation was higher (i.e. in the open and when owls were present). When more seeds were added, the gerbils became more risk averse (i.e. they devoted more time to predation avoidance and spent less time foraging).

Herbivores often forage across landscapes that differ considerably in terms of predation risk. These have been termed 'landscapes of fear' (Laundré et al. 2001). Using a grid of artificial food patches and measuring GUDs, Shrader et al. (2008) mapped landscapes of fear of free-ranging domestic goats *Capra hircus* on three substrates (open plains, sandy riverbeds, rocky hillsides) in the arid Riemvasmaak area of the Northern Cape province of South Africa. They first compared GUDs to landscape variables. Goats had lower GUDs on open ground, indicating that they preferred feeding on open ground with a firm substrate compared to a sandy riverbed or a rocky hillside (Fig. 6.3). This may be related to escape potential (it is easier to escape across an open plain than from riparian areas or rocky hillsides) and the occurrence of sites from where they can be ambushed (leopards often ambush goats by hiding among rocks or drop down on them from large trees). These authors then increased predation risk by adding smells of predators in the form of predator dung and urine into the habitats. They found that feeding effort declined across all three habitats. An important factor was the presence of better sightlines that increased predator detection and allowed individuals to see fellow group members because increased vigilance by the entire group served to warn individuals of the presence of predators (Shrader et al. 2012). In a similar vein, Kotler et al. (1999) and Druce et al. (2006) found that rock hyraxes, *Procavia capensis*, foraging in the arid Augrabies National Park in South Africa foraged at intermediate distances from their burrows because they used individual hyraxes as sentinels. These sentinels had the best sightlines at intermediate distances from their burrows. Van der Merwe and Brown (2008), working in the same area as Kotler et al. (1999) and Druce et al. (2006), found that Cape ground squirrels, *Xerus inauris*, had lowest GUDs closest to their burrows, indicating their preferences for foraging there. Van der Merwe and Brown (2008) recognized that, because ground squirrels can burrow quickly and prefer to forage where there is most food, these animals may choose burrow sites based on food availability unlike rock hyraxes that are constrained by the availability of rocky cliffs to construct their burrows.

A fascinating example of the interaction between flea parasitism and predation risk occurs in Allenby's gerbils (*Gerbillus andersoni allenbyi*) (Raveh et al. 2011). These Negev Desert gerbils are parasitized by fleas such as *Synosternus cleopatrae*

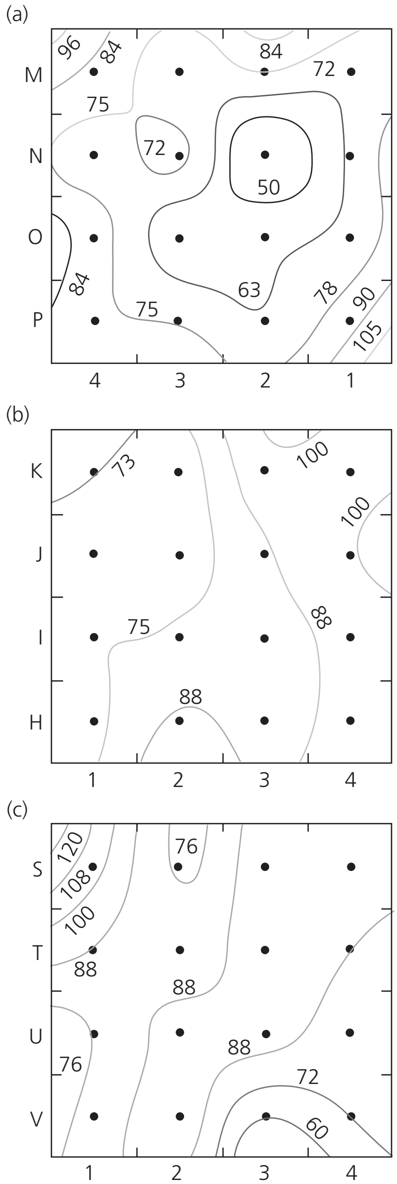

Fig. 6.3 Landscapes of fear for goats foraging in the arid Riemvasmaak area of the Northern Cape, South Africa, across the open ground (a), sandy riverbed (b), and hillside habitats (c). Lines represent contours of feeding effort (i.e. giving-up densities (GUDs). Lower GUDs, represented by dark lines, indicate greater preference for an area. The position of the 4 × 4 grid of feeding trays are represented with solid dots. Overall, goats preferred feeding in the open ground habitat (note the lower GUDs) than either the sandy riverbed or hillside.

Source: From Shrader et al. 2008. With kind permission of Elsevier.

pyramidis, and spend considerable time grooming to remove the ectoparasites (Krasnov et al. 1998). However, no detrimental energetic or immunological effects of the ectoparasites have been recorded in adult Allenby's gerbil (Khokhlova et al. 2004; Hawlena et al. 2006). Raveh et al. (2011) manipulated flea infestation on gerbils and introduced predation risk in the form of a fox. They showed that gerbils responded to fleas by leaving resource patches at higher GUDs (Fig. 6.4). When flea-ridden, gerbils also abandoned using vigilance to manage risk and relied mainly on time allocation. Thus, having fleas imposed a foraging cost similar to the risk of predation from foxes and perhaps larger in magnitude. The fleas reduced the gerbils' foraging abilities and changed how they managed predation risk. Raveh et al. (2011) hypothesized that fleas reduce the attention that gerbils otherwise have for foraging and predator detection; they truly are being driven to distraction. This is clearly a major cost of ectoparasitism.

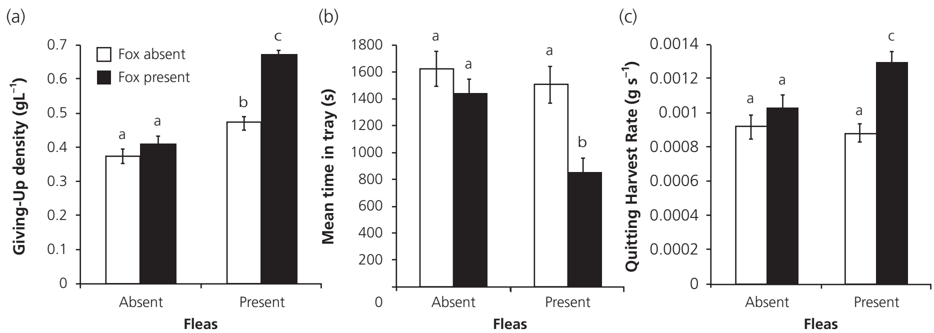

Fig. 6.4 Mean giving-up densities (GUDs) (a), time spent in the patch (b), and quitting harvest rates (c) under fox and flea treatments. Black bars indicate fox presence. Error bars reflect standard error. Letters above the bars reflect significant differences (where different letters appear) according to Tukey's (honest significant difference) HSD. The GUDs are based on data from all of the seed trays; the time in patch and quitting harvest rate data are based on data from trays with an electronic reader that automatically recorded the time of visit to the tray, the identity of the forager, the duration of the visit, and the cumulative duration of the time spent in the tray.

Source: From Raveh et al. (2011). With kind permission of Blackwell.

6.3 Apparent predation risk

Morris (2009) was the first to suggest that interference competition may mimic the effect of predation risk on foragers. If subordinate individuals exhibit a high degree of vigilance towards their dominant competitors, this may well reduce their foraging efficiency, and moreover it may also come at the expense of vigilance against predators (especially if these predators require vigilance via different sightlines (Shrader et al. 2008; Embar et al. 2011)). This may cause subordinate individuals to select alternative patches and habitats that do not have the same dominant competitors (Halliday and Morris 2013). Morris (2009) called this change in patch use or habitat selection apparent predation risk. Berger-Tal et al. (2015) investigated apparent predation risk in Allenby's gerbils, *Gerbillus andersoni allenbyi*. They used comparisons of solitary and paired gerbils. There was strong interference competition in the pairs of gerbils. This interference competition reduced the amount of time that the gerbils spent foraging. They found that this was due to time spent observing their competitors, which is what Morris (2009) called *apparent predation risk*. Interference competition reduced the success of gerbils foraging in pairs by more than 50% (Fig. 6.5). Berger-Tal et al. (2015) consider this to be the tragedy of the commons (*sensu* Hardin (1968); see Rankin et al. (2007)) because each individual's investment in competition reduced the success of all individuals in the group, including that of itself. At first glance this appears paradoxical but, if viewed in evolutionary terms, the competitive behaviour of each individual will be selected for if it leads to increased fitness relative to that of other individuals in the group (assuming an individual selection scenario; Wade et al. 2010).

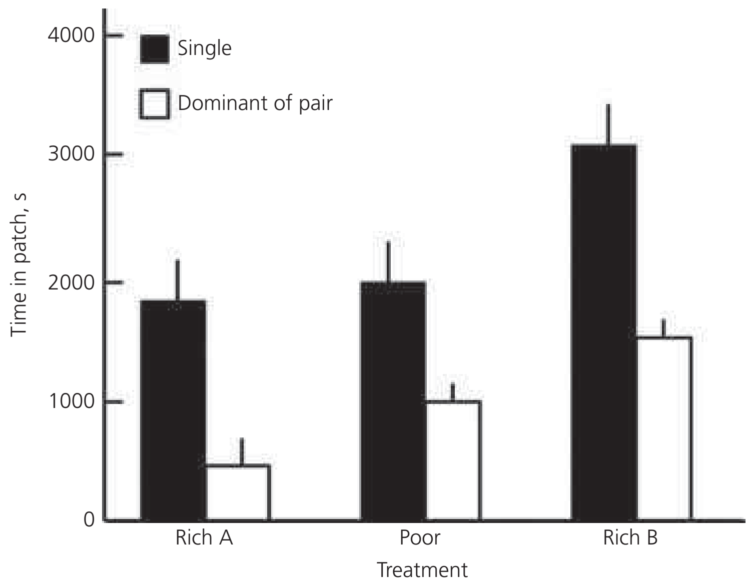

Fig. 6.5 A comparison of the mean time that single *Gerbillus andersoni allenbyi* gerbils spent in the feeding trays (black bars), and the time that the dominant individuals within gerbil pairs spent in them (grey bars), as a function of the different environmental quality treatments. During *Rich* period A, all trays contained 4 g of millet seed for three nights. This period was followed by a three-night *Poor* period in which the amount of seeds were reduced to 1 g in three trays with one tray containing 4 g of seeds. Thereafter, this was followed by three night of *Rich* period B with seed trays once again containing 4 g of millet seeds. Error bars represent standard errors.

Source: From Berger-Tal et al. (2015). With kind permission of the Ecological Society of America.

6.4 Priority effects

A number of studies have shown that priority effects can be very important in ecosystems. A priority effect indicates that the order in which a species enters a system affects the outcome of the interactions. This can apply to either competition or predation. For example, Blaustein and Margalit (1996) found that the 'winner' of the interaction between a tadpole or a larval mosquito in ephemeral desert pools depended on the species that arrived there first. If the tadpole *Bufo viridis* arrived in a pool first, it would consume the mosquito larvae that arrived there subsequently. Conversely, if the mosquito larvae *Culiseta longiareolata* arrived there first, they would consume the tadpoles. Dayton and Fitzgerald (2001) found a similar interaction between two toad species in desert pools, *Spea couchii* and *Bufo speciosus*. Dayton and Wapo (2002) found that oophagy (egg-eating) by *Spea couchii* tadpoles on their conspecifics occurred. Temporary pools may create competitive scenarios for animals living in these pools because of their ephemeral nature. Thus, competition may develop for the limited resources in the pool (densities of *Spea couchii* may exceed 1000 individuals per litre). Competition or predation would benefit the individual, resulting in more individuals passing on their genes to the subsequent generation. Cannibalistic oophagy may benefit the tadpoles because eggs can't bite back and time to metamorphosis of the tadpoles may be reduced because of increased food intake. This may also explain why there are priority effects between *Spea couchii* and *Bufo speciosus*. Priority effects can be thought of as a form of temporal resource partitioning. However, there is a problem in assigning causation. Does a priority effect occur because of competition or in spite of it?

6.5 Spiders

In a single wadi system in the Negev Desert (Israel), Lubin et al. (1993) and Ward and Lubin (1993) examined the effects of web relocation (a form of habitat selection) on the fitness of two spiders, *Latrodectus revivensis* (Theridiidae) (Fig. 6.6), a widow spider that feeds on cursorial prey such as darkling beetles, and *Stegodyphus lineatus* (Eresidae) (Fig. 6.7), which traps flying insects. They found that both spider species moved nests relatively frequently as juveniles, always moving to nests that could accommodate their progressively larger bodies. Ward and Lubin (1993) found that food-supplemented *Stegodyphus* spiders bred earlier and had more young than non-supplemented spiders. Also, these spiders moved more frequently if close to areas with greater annual plant densities—which attracted aerial insects to their webs. In contrast, there was a negative effect of dispersal on *Latrodectus* spiders; mortality increased to about 40% (Lubin et al. 1993) from an overall level of about 2.5% in the nest. Nonetheless, *Latrodectus* spiders had better body condition and had greater reproductive success when they relocated their nests. Thus, both studies, albeit on spiders with different types of prey, showed the pivotal role of food availability on activity and reproductive output. Similar results were obtained in North American

Fig. 6.6 Web of *Latrodectus revivensis.*
Source: Photograph courtesy of Yael Lubin.

Fig. 6.7 Web of *Stegodyphus lineatus.*
Source: Photograph courtesy of Trine Bilde.

deserts by Riechert (1981) and Riechert and Harp (1987) for the sheetweb-building spider *Agelenopsis aperta* (Agelenidae) and in the Australian desert spider, *Geolycosa godeffroyi* (Lycosidae) (Humphreys 1973).

Shadow competition for food may occur when sedentary foragers closer to a source of food reduce the prey's availability to those further away (Lubin et al. 2001). This process should increase with the size and density of a group of predators. Lubin et al. (2001) tested for shadow competition in a burrowing spider, *Seothyra henscheli* (Eresidae), which forages mainly on ants, in the Namib Desert (see Chapter 4 for further reference to the thermal niche of this spider). Individual spiders occurring inside or on the periphery of clusters were compared to solitary spiders in a natural population. Spiders in the population grew more slowly in clusters than did solitary spiders. The greatest effect was at highest densities, where nearly all spiders maintained active webs, indicating a state of hunger. Ants reach spider webs at different locations within the patches of different densities. Simulation modelling confirmed that shadow competition adequately explained the patterns of foraging and growth of sedentary foragers such as these spiders (Lubin et al. 2001). What causes spiders to keep to the centre of a cluster? There are two reasons, which may not be mutually exclusive:

1. These spiders occur in dune sand and tend to keep close to the maternal burrow because of uncertainty over dune stability further away (Henschel and Lubin 1992, 1997). Peripheral webs would be more susceptible to dune instability than those in the centre.
2. Predation on spiders, especially by another spider, *Palpimanus stridulator* (Palpimanidae) (Henschel and Lubin 1992), should be higher on the periphery than in the centre because of a 'selfish herd' effect (Hamilton 1971). In other words, it will always be better for a spider to occur in the centre of a group to avoid being eaten on the outside of the group. Indeed, survival was lower for peripherally located spiders, despite the higher growth rate (Lubin et al. 2001).

6.6 Scorpions

A few desert arachnids may specialize on certain prey types. For example, in the Kara Kum Desert in central Asia, *Minosiella intermedia* (Gnaphosidae), which is the most common spider in rodent burrows, specialized and accepted only fleas and small scarab beetles (Krivokhatsky and Fet 1982). Two scorpions are specialists. The Australian species *Isometroides vescus* focuses on trapdoor spiders (Ctenizidae) (Main 1956) and the Saharo-Arabian Desert species *Scorpio maurus* takes up to 77% of its food from the terrestrial isopod *Hemilepistus reaumuri* (Shachak 1980). Indeed, the latter species may often place their burrows as close as 10 cm from the nearest isopod burrows (Shachak 1980). However, Polis and McCormick (1986) found that scorpions more often took prey of different sizes depending on their own body sizes. This is known as intraguild predation, and is consistent with the gape-limitation hypothesis (Zaret 1980); that is, the mouth size of an organism necessarily limits the size of the prey that they can ingest. Although this is not universally true (e.g. the spider *Latrodectus hesperus* can catch scorpions and sun spiders (also known as wind spiders; order Solifugae) that are several times larger than themselves (Polis and Yamashita 1991)), many scorpions often change size dramatically during development. For example, growing *Paruroctonus mesaensis* increase 40–60 times in mass. Instar 2 scorpions eat prey that average 5 mm in length, whereas adults consume prey that are about three times larger, 66% of which are different scorpion species (Polis and

Yamashita 1991). Indeed, the effects of age structure, trophic opportunism, cannibalism, and intraguild predation on other predatory arthropods are the norm rather than the exception.

Polis and McCormick (1986) removed about 6,000 scorpions from 300 × 100 m^2 plots over 29 months in the Coachella valley, Mojave Desert (North America). They found that the number of spiders increased in the removal plots (Fig. 6.8). This could be explained either by exploitation competition (i.e. with no scorpions present there was more prey remaining for spiders to consume) or direct intraguild predation. They found no effect of exploitation competition because prey (spiders) did not increase in number in the removal plots and spiders did not grow bigger in these plots. Rather, scorpion predation on spiders (intraguild predation) explained the difference in spider numbers. Polis and McCormick (1986) record 'looping mutual predation', where one species eats another and vice versa as rather common in the Coachella valley in the Mojave Desert (North America). Scorpions eat spiders and solifuges, spiders eat scorpions and solifuges, etc. A similar result to the Coachella valley study was recorded in the Namib Desert on *Acacia erioloba* trees in the Kuiseb River. In that study, *Gandanimeno eresus* (Eresidae) spider populations were reduced by 42% when the scorpion *Uroplectes otjimbinguensis* was added and increased by 2.9 times when the same scorpion was removed (no statement of numbers of scorpions added or removed was given; reported by Polis and Yamashita (1991)).

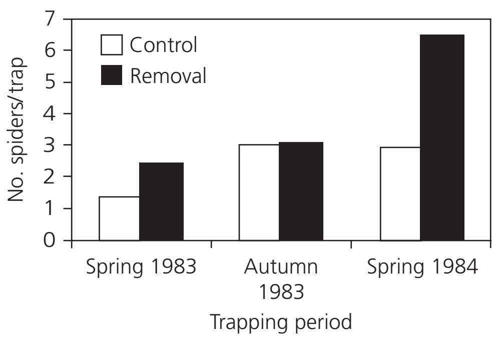

Fig. 6.8 Polis and McCormick (1986) removed about 6000 scorpions from 300 × 100 m^2 plots over 29 months. They found that the number of spiders increased in the removal plots in the spring of 1983 and 1984.

Source: Modified from Polis and McCormick (1986). Kind permission of the Ecological Society of America.

6.7 Visually hunting predators

Kotler (1984) showed that moonlight was important for visually hunting predators. By adding lanterns to a site in the Great Basin Desert (North America), he showed that rodents had lower foraging activity than near control (i.e. unlit) sites (see also Price et al. 1984). This effectively demonstrated that there should be a difference between full moon and new moon nights, as he also found (Fig. 6.9). This has subsequently been shown on a number of occasions (e.g. Hughes and Ward (1993) in the Namib Desert (Africa), and by Kotler et al. (1994, 2004) in the Negev Desert (Israel)). For example, Hughes and Ward (1993) showed that gerbils in the Namib Desert have lower GUDs on new moon (dark) nights and close to cover—that is, the patch is more valuable when predation risk is low, so they stay there longer and eat more (Fig. 6.10).

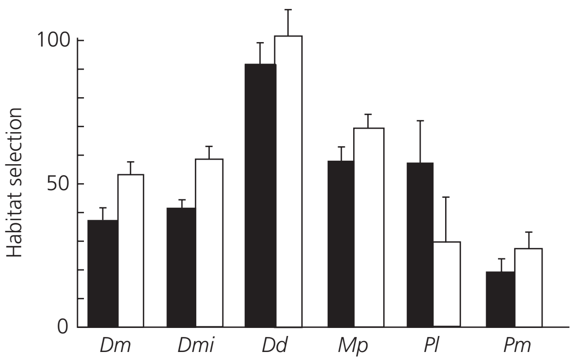

Fig. 6.9 Kotler (1984) showed that illumination was important for visually hunting predators. By adding lanterns to a site in the Great Basin Desert (North America), he showed that rodents had lower activity (i.e. showed greater predation risk) than near control sites. *Dm* = *Dipodomys merriami; Dmi* = *Dipodomys microps; Dd* = *Dipodomys deserti; Mp* = *Microdipodops pallidus; Pl* = *Perognathus longimembris*; and *Pm* = *Peromyscus maniculatus*. Open columns = control data; closed columns = experimental data.

Source: From Kotler (1984). With kind permission of the Ecological Society of America.

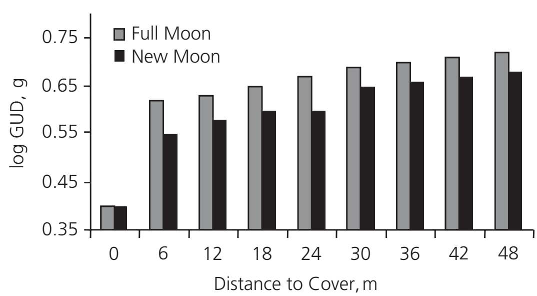

Fig. 6.10 Gerbils in the Namib Desert have lower GUDs on new moon (dark) nights and close to cover—that is, the patch is more valuable when predation risk is low, so they stay there longer and eat more.

Source: From Hughes and Ward (1993). With kind permission of Elsevier.

6.8 Snakes, scent-hunting predators

Many members of the Reptilia are able to use vision to hunt for their predators. These include chameleons, geckos, iguanas, and agamas. It is only the autarchoglossans (also called the 'independent tongued' reptiles) that are capable of picking up heavy, non-airborne chemicals from surfaces with their tongues (Vitt and Pianka 1994). The tongue deposits these chemicals on the vomeronasal organ, from where the information is obtained to enable the animal to assess the suitability of the prey item for capture. Bouskila (1995) has stressed that there is an important difference between snakes (and other scent-hunting vertebrate predators) and visually hunting vertebrate predators such as owls, foxes, coyotes, and jackals (see also the Hughes et al. (1994) study in the Namib, where owls and jackals were the main predators). One of the consequences of this difference in hunting mode is that snakes are sit-and-wait predators that predominantly hide in bushes, while owls and other visually hunting predators hunt primarily in the open. Bouskila (1995) found that when sidewinder snakes (*Crotalus cerastes*) in the Mojave Desert (North America) were the main predators, the kangaroo rats, *Dipodomys deserti* and *Dipodomys merriami*, preferred to forage in the open and avoided the bush (Fig. 6.11). This microhabitat choice is the opposite of that preferred by the sidewinder snake in this habitat, which prefers the bush. Moreover, this is also the opposite behaviour of the gerbils (mentioned earlier) studied by Kotler et al. (2004) in the Negev Desert (Israel) and the gerbils in the Namib Desert studied by Hughes et al. (1994) (see Chapter 5), because they prefer open microhabitats. Interestingly, the dominant kangaroo rat species (*Dipodomys*

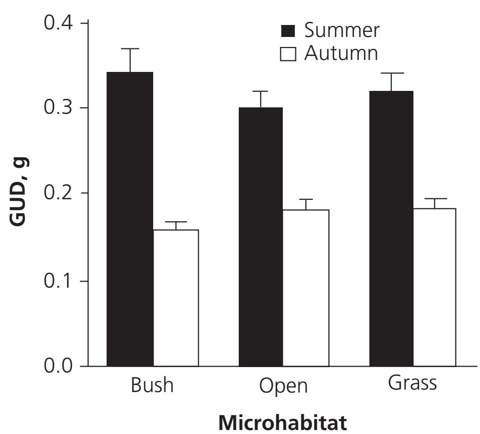

Fig. 6.11 Bouskila (1995) found that when sidewinder snakes (*Crotalus cerastes*) in the Mojave Desert (North America) were the main predators, the kangaroo rats, *Dipodomys deserti* and *Dipodomys merriami*, preferred to forage in the open and avoided the bush.

Source: From Bouskila (1995). With kind permission of the Ecological Society of America.

deserti) foraged more in the microhabitat avoided by the snake but the subordinate kangaroo rat species, *Dipodomys merriami*, chose the same microhabitat as the snake to avoid competition. This is yet another way that competition and predation interact.

Another interesting feature of Bouskila's (1995) study is that there was no effect of moonlight on foraging activity when snakes were the main predators; that is, kangaroo rats did not forage more on dark nights than on moonlit nights. This is contra examples provided by Kotler (1984) and Price et al. (1984) in North American deserts and Hughes and Ward (1993) in the Namib Desert, among others. All these latter cases involved visually hunting predators such as owls, foxes, and jackals. Bouskila (1995) observed that if the snakes were inactive (in autumn, on account of low temperatures), then there was a preference for foraging on dark nights. This means that desert rodents do not have many places to hide in the summer months because visually hunting predators occupy the open microhabitats and scent-hunting predators occupy the bush microhabitats. In contrast, in the winter months, rodents become averse to using moonlit nights, because snakes are ectotherms and hibernate during the winter, but visually hunting predators such as owls and large mammals are still active because they are endotherms.

6.9 Keystone predation

Although keystone species can easily be described for competitive and facilitative scenarios (e.g. Munzbergova and Ward 2002; Schleicher et al. 2011b; see Chapter 5), it is actually for predation that Paine (1966) first described it. Keystone predators are defined as having a greater effect than that explained by density or dominance alone (Peckarsky et al. 2008). Paine (1966) described a simple system with relatively few species. Once systems become more complex, there are many potential keystone predators (Paine 1980). In species-rich communities, dominance by a single predator or a few predators may be sufficient to explain predation (i.e. it is based on density rather than unique species with stronger effects). In North America, Henke and Bryant (1999) reduced the densities of coyotes *Canis latrans* from 0.12 to 0.06 km^{-2} in two treatment plots and kept two plots constant at about 0.14 km^{-2} in the Chihuahuan Desert (350 mm mean annual rainfall). Each plot was 5000 ha in size. They found that the treatment plots had lower species richness and lower diversity of rodent species. Without coyote predation, Ord's kangaroo rat (*Dipodomys ordii*) became the most abundant rodent in shrubland and was the only rodent species caught in grassland after 12 months of coyote removal. Rodent density and biomass, black-tailed jackrabbit (*Lepus californicus*) density, and the relative abundance of badgers (*Taxidea taxus*), bobcats (*Felis rufus*), and gray foxes (*Urocyon cineroargenteus*) increased on treatment sites. Thus, there is strong evidence for a mesopredator-controlled coexistence of species and, consequently, evidence for keystone predation.

Johnson et al. (2007) have shown that 18 mammal species have gone extinct since European settlement began in Australia. The causes of these extinctions are not entirely clear, although many sources have blamed the introduction of red foxes (*Vulpes vulpes*) and cats (*Felis catus*). Cats are widespread throughout Australia and red foxes occur everywhere except in the northern tropics. Overkill is claimed to be the main threat for small mammals in Australia. Australia's largest extant predator is the dingo (*Canis lupus dingo*), which was introduced to Australia by native Australians (Glen et al. 2007). Where dingoes are locally abundant, cats and red foxes are rare (Newsome 2001; Glen and Dickman 2005; Sutherland et al. 2011; Gordon et al. 2015). Dingoes may limit the populations of these two smaller introduced predators and may directly cause their mortality (O'Neill 2002; Mitchell and Banks 2005). European settlers have killed dingoes, especially in sheep-farming areas. Johnson et al. (2007) tested whether, in areas where dingoes have remained abundant, native marsupial species have remained more common than in areas where dingoes have been eliminated. They showed that the dingo, the top predator, is indeed limiting the presence of introduced mesopredators (red foxes and cats). Gordon et al. (2015) found evidence that suppression of abundance and activity of a mesopredator (the feral cat) by an apex predator (the dingo) has positive effects on the abundance and the foraging efficiency of a desert rodent, *Notomys fuscus*, in the Strzelecki Desert, in central Australia. They too used giving-up densities (GUDs) to estimate patch use by *Notomys*. They developed an a priori structural equation model (SEM) that they tested for evidence supporting mesopredator release. They manipulated predators' access to food patches and found evidence that apex predators provide small prey with refuge from predation by showing that *Notomys fuscus* rodents increased their habitat breadth and use of 'risky' food patches where an apex predator was common and mesopredators were rare (Fig. 6.12). The Gordon et al. (2015) study shows that apex predators (dingoes) have a suppressive effect on mesopredators (foxes and feral cats) which alleviates both mesopredators' consumptive and non-consumptive effects on prey. In another study, Sutherland et al. (2011) tested whether varanid lizards in Australia were mesopredators and whether there could be mesopredator release. Varanids share a similar niche with that of eutherian carnivores in the Old World and carnivorous marsupials in Australia. Small varanids are only found east of Wallace's Line (Sweet and Pianka 2003), primarily in Australia and the islands of southeast Asia, where eutherian carnivores (such as the dingo) have only recently arrived. This is suggestive of strong competitive interactions between these two groups, where small varanids are unable to persist in the presence of eutherian carnivores as they are vulnerable to predation throughout their ontogenies. Sutherland et al. (2011) performed a meta-analysis and found that there was indeed a high degree of overlap in the diets of varanids and the introduced eutherian carnivores such as foxes, feral cats, and dingoes.

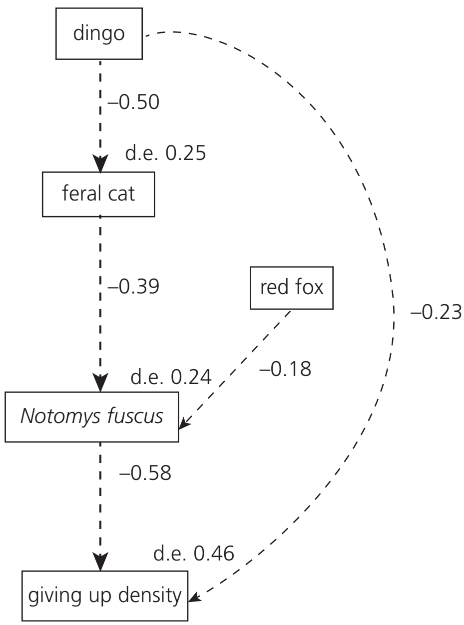

Fig. 6.12 The most parsimonious structural equation model (SEM) showing the effects on the GUDs of the Australian desert rodent *Notomys fuscus*. Dashed arrows represent negative pathways and are weighted by standardized path coefficient estimates. The SEM suggests that feral cat activity was higher where dingo activity was low. *Notomys fuscus* abundance was higher where cat and fox activity were low and dingo activity was high. The GUD of *Notomys fuscus* increased with increasing dingo activity and *Notomys fuscus* abundance. The abbreviation d.e. is the deviance explained by each variable.

Source: From Gordon et al. (2015). With kind permission of the Royal Society of London.

6.10 Animal parasites and parasitoids

Parasitism has been little studied in deserts, largely because many researchers have believed that the harsh environment has limited the ability of parasites to invade these habitats. Recent work suggests that this may be a misconception and that parasite–host interactions may be as important in deserts as they are elsewhere (Lafferty and Kuris 2002; Krasnov 2008). I will consider some fascinating examples of parasitism, such as parasitoids controlling the body temperatures of their hosts to ensure the survival of their offspring and host choice in fleas being controlled by the off-host environment (contra conventional wisdom that it is the host's physiology that limits the success of the parasite).

What is the difference between parasites and parasitoids? Parasites typically do not kill their hosts but can suppress their metabolism severely while parasitoids do ultimately kill the host. The host to the brood parasite raises the parasite's young once they have hatched.

6.10.1 Parasites

Parasites may be divided into endoparasites, which occur inside the body of the host and that are typically small (although tapeworms, for example, can be extremely large) and ectoparasites, which are external (Lafferty and Kuris 2002). Parasites can be extremely abundant and may be as much as four times more common than other organisms in an ecosystem (Lafferty and Kuris 2002). Krasnov et al. (1997) have studied the effects of ectoparasites, specifically fleas (Siphonaptera; Fig. 6.13) on rodents in the Negev Desert of Israel. Fleas are not as specific in their host preferences as one might expect. A single flea species may parasitize several rodent host species. In the fleas studied by Krasnov et al. (1997), they have also shown that it is not only the host and its immediate environment (e.g. the burrow of the host) that limits the numbers or presence of fleas but also the general environment of the desert that is important. For example, there was complete replacement of one flea species (*Xenopsylla conformis*) with another (*Xenopsylla ramesis*) on the same rodent hosts (*Meriones crassus* and *Gerbillus dasyurus*) at either end of a steep precipitation gradient in the Negev Desert (Krasnov et al. 1998). This replacement was due, partly, to abiotic features of the habitats such as ambient temperature, humidity, and substrate type. Yet other flea species in this desert depend on the host identity–habitat identity

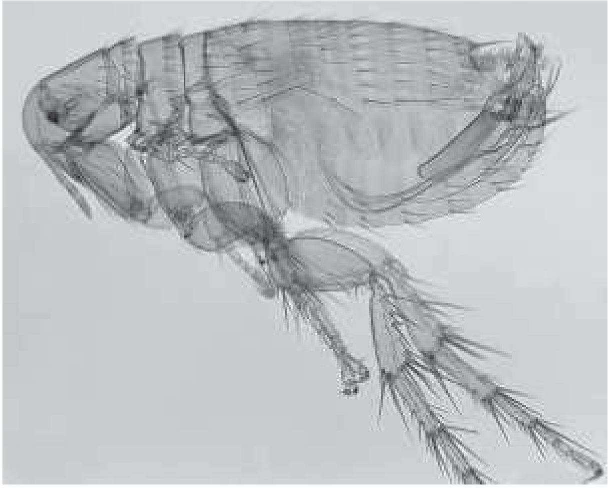

Fig. 6.13 A flea (*Xenopsylla dipodilla*) from the Negev Desert, Israel.

Source: Photograph courtesy of Michael W. Hastriter, Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, U.S.A.

interplay (B. Krasnov, pers. comm.). Krasnov (2008) has found that temperate and desert habitats may differ in host–parasite relationships, particularly for pre-imago fleas where the burrow is the ultimate habitat, because of the more extreme nature of the desert environment. Most desert rodents and insectivores dig deep burrows to avoid environmental extremes while temperate rodents and insectivores occupy above-ground or shallow burrows. Between-habitat differences in the desert environment are likely to be more extreme than in temperate environments. An alternative explanation is that interspecific visits are more frequent in temperate habitats than in desert habitats because of the higher densities of small mammals in temperate habitats, resulting in greater host-switching (Krasnov 2008).

An interesting case of an endoparasite parasitizing a toad occurs in ephemeral Arizona (U.S.A.) pools in the Sonoran Desert. The parasite is a polystomatid flatworm, *Pseudodiplorchis americanus* (Monogenaea, Platyhelminthes), that parasitizes a desert toad, *Spea couchii* (Tinsley 1999; Tinsley et al. 2002). The toad hibernates for 9–10 months and only enters the water for a few hours to a few days a year to breed. The parasite lays eggs at the time that the toads are spawning, allowing the larvae only that short period to infect other mature adult hosts while they too are spawning. It is too risky for the parasites to infect the tadpoles instead of the adults because of the high probability that the pond may dry out before the tadpoles mature.

6.10.2 Parasitoids

Ward and Henschel (1992) have shown that there is a unique interaction that occurs between the parasitoid *Pseudopompilus humboldti* (Pompilidae, Hymenoptera) and its spider prey *Stegodyphus lineatus* in the Negev Desert of Israel. The pompilid wasp typically alights on the capture web of the spider and gently shakes it, giving the appearance that there is a prey item attached to the web. The spider, which hides in its dense silk nest, runs down to investigate. The pompilid attacks the spider and anaesthetizes it. It then positions the spider in the entrance of the nest, allowing the egg it has just laid on the spider to develop there, rather than pushing it back into the nest, where it would be invisible to predators or scavengers. Ward and Henschel (1992) performed a simple experiment to test whether positioning at the nest entrance was because of the high ambient temperatures that the spider would reach inside the nest in the heat of the day. They pushed some of the spiders that were anaesthetized back up into the nest and the rest they manipulated but left on the nest entrance. The mean ambient temperature of spiders inside the nest was on average 6°C higher than that of spiders left on the nest entrance during the heat of the day. More importantly, all spiders left on the nest entrance survived and all the spiders in the nest died, presumably from overheating. Thus, this is an effective way that pompilid wasps can protect their offspring by controlling temperature indirectly via host manipulation. This also demonstrates an adaptive trade-off between thermoregulatory requirements and predation risk.

Henschel (1990) showed in the Namib Desert that pompilid wasps can attack spiders that burrow in shifting dunes. These spiders (*Carparachne aureoflava*, Heteropodidae) have a unique mechanism to avoid this parasitism, namely, when exposed by the wasp they wheel down the dune face to escape parasitism, relying on gravity for momentum (Fig. 6.14). They may rotate between 600 and 2650 rpm and achieve speeds that can be as much as 0.5–1.5 m s^{-1}, depending on body size and steepness of the dune slope. This strategy appears successful; spiders that wheeled to escape avoided parasitism while those that did not failed to escape the pompilid spider's parasitism.

Fig. 6.14 *Carparachne aureoflava* spiders (Heteropodidae) have a unique mechanism of wheeling down the dune face to avoid parasitism by pompilid wasps, relying on gravity for momentum.

Source: Photograph courtesy of Joh Henschel.

7 Plant–Animal Interactions in Deserts

Plant–animal interactions are as important in deserts as they are in any other ecosystem. Although it is likely that abiotic factors have greater influence in deserts than in other ecosystems, biotic factors are nonetheless very important. Desert plants and animals interact in ways that have strongly influenced their respective evolutionary trajectories. This chapter begins with herbivory because of its widespread impacts, many of which are presumed to be negative. It then considers some other important aspects of desert plant–animal interactions, with a focus on pollination and seed dispersal. Of the various forms of pollination, the chapter will focus on the yucca moth–yucca and senita moth–senita cactus mutualisms. With regard to the role of animals in seed predation and seed dispersal, this chapter will consider the effects of small mammals and ants on seed abundance, and the role of large mammals in dispersing the seeds of keystone *Acacia* species (Milton et al. 1999; Munzbergova and Ward 2002). These examples illustrate how—despite the large physiological stresses that plants and animals undergo to live in a desert (and perhaps because there are relatively few organisms that can withstand desert environments)—biologists have made noteworthy discoveries in the importance of plant–animal interactions for ecosystem function in deserts (e.g., Goldberg and Turner 1986; Westoby 1989; Milton 1991; Markow 1995; Pellmyr et al. 1996; Vesk et al. 2004; Diaz et al. 2007; Kohl et al. 2014).

7.1 Herbivory

It has been argued that herbivory by mammals does not contribute significantly to arid ecosystem functioning and biodiversity maintenance (reviewed by Noy-Meir 1973). Instead, abiotic factors such as high temporal and spatial variation in rainfall are suggested to be the most important factors for the ecology of arid ecosystems. There is a strong negative correlation between the coefficient of variation in mean annual rainfall among years and median annual rainfall of arid regions, which results in high variability in the germination of annual plants and high variability in the growth of perennial plants (Ward 2001, 2005a). Similarly, spatial variation in rainfall is high and is not correlated with distance among sampling points (Ward et al. 2000a, 2004). This variability in rainfall results in high spatio-temporal variability in plant abundance and availability to herbivores. Ward et al. (2000a) showed

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that, in the Negev Desert of Israel, only 1% of plant species were present in permanent plots in all years and approximately half the plant species were found only once in 10 years (Fig. 7.1).

Temporal variation in plant species richness can also be quite large; note the relationship between the coefficient of variation in plant species richness and total plant species richness (Fig. 7.2). This relationship is an envelope effect in that there is more variability when the total number of species is small (because there may be various reasons (such as edaphic variability) why total species numbers are limited) and it decreases as species richness increases, probably being limited by precipitation (Fig. 7.2).

Further contributing to spatial variation, in some arid regions, is the pattern of 'contracted vegetation' (*sensu* Whittaker 1975) whereby plants are almost entirely restricted to ephemeral watercourses. Another confounding factor is that geological substrates vary considerably among arid regions, particularly in their nutrient status and water retention capacities (Landsberg et al. 1999a; Ward 2005a). Patchy nutrients and water availability lead to considerable differences in plant composition and nutritional quality among habitats (Stafford Smith and Morton 1990; Ward and

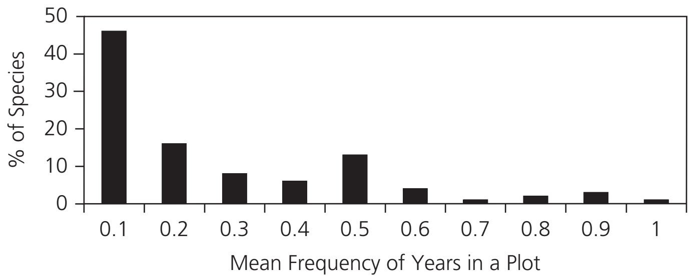

Fig. 7.1 Histogram of frequency of occurrence of plant species over time in Makhtesh Ramon, Israel. Most species rarely occur in any single plot.

Source: From Ward et al. (2000a). Kind permission of Springer.

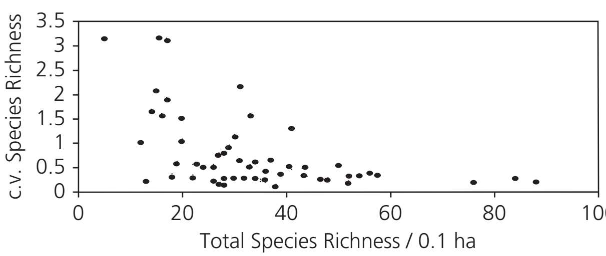

Fig. 7.2 Temporal variation in 0.1 ha vegetation plots in Makhtesh Ramon, Israel. c.v. = coefficient of variation.

Source: From Ward et al. (2000a). With kind permission of Springer.

Olsvig-Whittaker 1993; Ward et al. 1993; Ward 2005a). The high spatio-temporal variability in the availability of plants to herbivores necessarily limits the numbers of herbivores that can be sustained in arid ecosystems, which is considered to limit their impacts on plant resources (Polis et al. 1999). Milchunas et al. (1988) predicted that a long evolutionary history of grazing results in the selection for regrowth following herbivory and for prostrate growth forms. In such communities, grazing causes rapid shifts between suites of species adapted to either grazing avoidance/tolerance or competition. In their global review, Milchunas and Lauenroth (1993) showed convincingly that evolutionary history of grazing had an effect on grazing responses inside and outside herbivore exclosures in North and South America (Fig. 7.3). What does this mean? Milchunas and Lauenroth (1993) infer that species that are highly palatable have been removed from the vegetation in areas with a long evolutionary history of grazing and only non-palatable species remain. Thus, there is no clear effect of grazing on changes in plant species composition. A possible reason for this is the *Narcissus effect* (*sensu* Colwell and Winkler 1984), which means that selection in the past has resulted in the extinction of all non-resistant/tolerant genotypes. Thus, all extant species are similarly resistant to herbivores, resulting in an absence of an effect of current herbivory on plant diversity (Ward and Olsvig-Whittaker 1993; Perevolotsky and Seligman 1998). Presumably, in such ecosystems, conditions seldom favour growth-dominated genotypes. Thus, only one (resistant/tolerant) genotype exists in these populations. Interestingly, re-examination of the same data for Africa and Asia (Ward 2005a) shows no such effect and indicates that grazing responses are positively correlated with mean annual rainfall in those studies (Fig. 7.3).

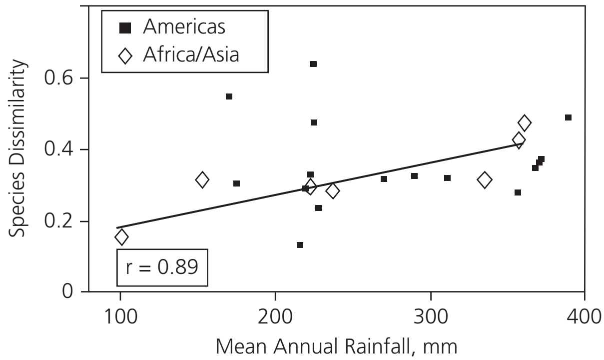

Fig. 7.3 Differences in species composition between grazed and ungrazed lands in arid ecosystems of the Americas and Africa and Asia (data limited to <400 mm rainfall from Milchunas and Lauenroth (1993)). There was no significant relationship between species dissimilarity and mean annual rainfall for the American comparison, while there was a significant relationship ($p < 0.001$) for the Africa and Asia comparison.

Source: Modified from Milchunas and Lauenroth (1993). With kind permission of the Ecological Society of America.

7.1.1 Grazing effects on species composition

Major differences between the effects of herbivores and carnivores on their food items are that herbivores seldom eat the entire food item and plants differ considerably in their quality. Plants can be of low quality because they contain low levels of energy and protein, have high levels of fibre, have high levels of defence compounds, and may have lots of mechanical defences (e.g. thorns). Herbivores can alter plant community composition by selecting dominant species, causing rare species to become more common, or by selecting rare species, increasing degree of dominance. However, this process usually does not affect diversity. Chesson (2000) developed a lottery model to explain how herbivores might affect plant diversity. In plant communities, spaces periodically become available when an inhabitant dies. Any species that has propagules ready at that time and place can occupy the space. This model makes the assumption that all plant species can increase when rare. Herbivores can increase the number of coexisting species by eliminating individuals of certain species, thereby freeing up space for other species that take their place opportunistically. If plants are avoided when rare, then the lottery model can explain coexistence of more species under herbivory (Fig. 5.1).

7.1.2 Long-term studies of the effects of large mammals on arid vegetation

What do field-based studies of the effects of herbivory by large mammals tell us about the effects of large mammals on vegetation of arid zones? Longer-term studies need to be considered when assessing the impact of herbivory in arid-zone vegetation because short-term studies might only show us the relatively trivial effects of differences in biomass consumption and show little in terms of changes in species composition. Although the following list is not intended to be exhaustive, such studies show inconsistent patterns in the response of arid vegetation to mammalian herbivory:

1. Goldberg and Turner (1986) analysed vegetation changes in nine permanent 100-m^2 plots first established in 1906 near Tucson, Arizona, U.S.A. (mean annual rainfall = 250 mm). These plots were fenced to exclude large herbivores in 1906 and were examined periodically until 1978. There were no consistent directional changes in vegetation composition between 1906 and 1978, despite large fluctuations in absolute cover and density of the species. For most species, and in most plots, the changes in absolute cover and density appear to have been a response to sequences of either exceptionally wet years or exceptionally dry years. Only two species, *Krameria grayi* and *Janusia gracilis*, appeared to increase over the study period—the former species is reported to be very palatable to livestock. A study comparing vegetation inside and outside the fenced areas following 50 years of protection showed that the total plant density was significantly higher within the fenced areas but there were no large differences in the composition of the vegetation (Blydenstein et al. 1957). As indicated earlier by Chesson (2000), it is changes in vegetation composition that are required to demonstrate changes in effects of herbivory rather than changes in biomass alone.

2. Ward et al. (1998, 2000a) and Saltz et al. (1999) examined the effects of reintroduced Asiatic wild asses, *Equus hemionus onager* (also called onagers or kulans), in 11 pairs of permanent plots in the central Negev Desert of Israel (mean annual rainfall = 56 mm) from 1992 to 1997. There has been considerable concern that the reintroduction of such a large equid (~200 kg) would cause habitat degradation through heavy grazing because large, hindgut fermenters are dependent on processing large quantities of low-quality forage. They found that fenced plots (i.e. wild asses excluded) had significantly higher plant cover than unfenced plots when differences in rainfall among plots were accounted for, although there were no significant differences in plant species richness, diversity, or dominance between fenced and unfenced plots. Three plant species showed significant increases in percentage cover in the fenced plots, and one species significantly increased in cover in the unfenced plots. Eight plant species invaded the fenced plots, three species invaded the unfenced plots, and one species disappeared from the unfenced plots during the study. Unfenced plots showed a directional change away from their original species composition (although plant species richness and diversity remained the same) while vegetation in fenced plots did not change over the period (Figs. 7.4a–c) (Ward et al. 2000a). These results indicate that herbivory by wild asses is causing a change in the relative abundance of certain species (unfenced plots) and that competitive effects in the protected plots have occurred when plants are protected from grazing.
3. Ward and Saltz (1994), Ward et al. (1997, 2000a), Saltz and Ward (2000), and Ruiz et al. (2001, 2002) studied the interactions between the dorcas gazelle, *Gazella dorcas*, and the desert lily, *Pancratium sickenbergeri*, in sand dunes in the central Negev Desert from 1990 to 2002. Gazelles dig in the sand to remove all or part of the bulbs of the lilies during the dry summer months, while in the winter months they consume the leaves. There are no leaves on the sand surface during the summer. From October to December they consume virtually all flowers when available—flowers have a 1:30,000 chance of surviving (Saltz and Ward 2000). They found that the gazelles entirely consume about 5% of the plants per annum, but may eat part of up to 60% of plants each year. Lily populations enclosed in 1994 (15 m × 15 m enclosures) now have about twice as many plants as populations outside the enclosures (478 vs 255 plants per plot), indicating a significant negative impact of herbivory.

7.1.3 Effects of herbivory on relationships among plant functional types

Some of the most interesting effects of herbivory on plant diversity are through the effects of selective herbivory on the relationships among plant functional types (Noy-Meir et al. 1989; Westoby 1989). Arid regions that experience summer rainfall are usually grass-dominated (e.g. Namib and Kalahari deserts, southern Sahara, Australia), while deserts with winter rainfall (e.g. Negev, Sonoran, and central Asian deserts) are usually dominated by asteraceous and other dicotyledonous annual

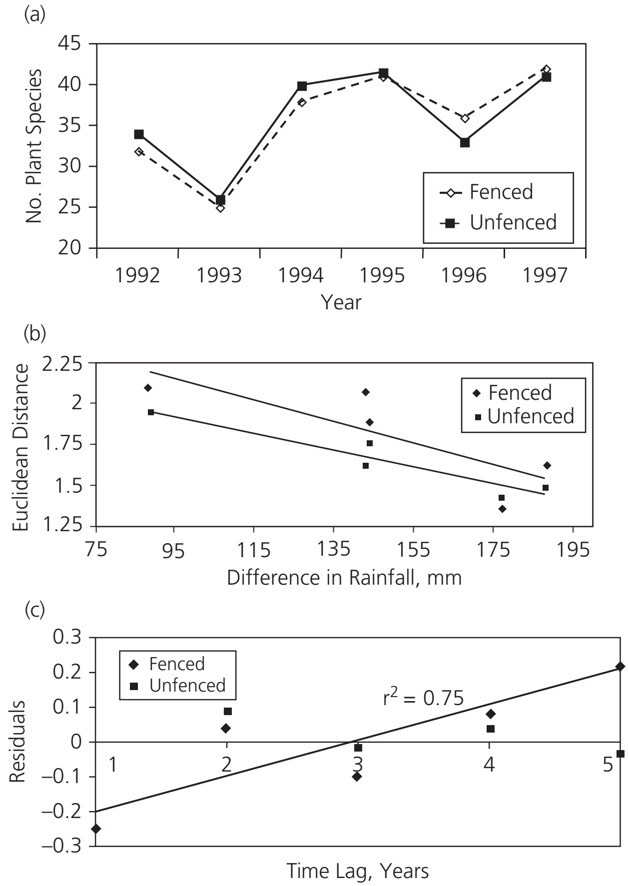

Fig. 7.4 Onager plots and plant species richness. (a) Herbivores appear to have little effect on plant species richness in the Negev Desert. (b) The change in Euclidean distance (overall changes among plots) over time is largely explained by differences in annual rainfall (r^2 = 0.80 (Fenced) and r^2 = 0.94 (Unfenced)). (c) When the effects of differences in rainfall were removed (= residuals), fenced plots deviated from their original composition (r^2 = 0.75), whereas unfenced plots stayed the same. *Y* axis = residuals from regression of Euclidean distance versus difference in rainfall between years.

Source: (a) From Ward et al. (2000a). With kind permission of Springer.

plants (Louw and Seely 1982; Shmida and Darom 1986). More conventionally, the most important changes in vegetation in response to herbivory occur in the relative abundance of tall and short annual and perennial plants (Noy-Meir et al. 1989; Ward 2005a).

The 'classical' theory of Dyksterhuis (1949) postulates that the main effect of grazers is through differential removal of plant parts among plant species which shifts the balance of relative species abundances. This is established in the ungrazed ('climax') state, mainly by competition for water, light, and nutrients, to a new stable balance, which depends on differential defoliation and regrowth. The relative abundance of some plants in a community decreases consistently in response to increased grazing intensity ('decreasers'), while that of others increases consistently ('increasers'), and some species only appear above a certain threshold of grazing intensity ('invaders'). Decreasers are plants with attributes that favour them in competition for space and other resources but disadvantage them under differential defoliation. Such attributes include erect tall shoots with elevated renewal buds, long growing season, perennial life cycles, and readily palatable and available to grazers (especially grasses and legumes) (Noy-Meir et al. 1989; Westoby 1989). Increasers (and invaders) are plants with at least some of the converse attributes: low or prostrate shoots with renewal buds close to or below ground, short growing season, annual or short perennial life cycle, and lower palatability to grazers due to chemical or morphological 'defensive' characters (especially forbs (non-legume dicotyledonous plants)).

The responses of many species in arid zones appear to be consistent with a modified version of the classical theory of grazing response, with its basic mechanism being a balance between competition and differential defoliation. Noy-Meir et al. (1989) and others (Diaz 2001; Vesk et al. 2004; Ward 2006) have shown that height decreases under increased grazing pressure because tall species receive most grazing pressure, perennials decrease because they are more available to herbivores, leaf size decreases because larger leaves provide larger bites for grazers, and high specific leaf area (high-SLA) species (which have thin, soft leaves) may be favoured by selective grazers (Vesk et al. 2004). Westoby (1989) found that, under intense, non-selective grazing, all species are grazed and high-SLA species may have an advantage because they have faster regrowth, which is due to quicker leaf turnover and a greater rate of regrowth per unit of carbon invested in leaf tissue (see also Vesk et al. 2004).

In Australia, Landsberg et al. (1999a) have shown that 'large erect tussocks branching above-ground' and 'small, sprawling basal tussocks' may potentially be recognized as functional grass types that are reliable indicators of light and heavy grazing, respectively. Heavy grazing is associated with an increased abundance of herbaceous forbs, many of which are facultative annuals in Australia. This trend is consistent with other studies that have shown increases in annual plants with heavy grazing (Noy-Meir et al. 1989; Friedel et al. 1990). The tendency towards a decrease in the relative abundance of grasses at heavily grazed sites has also been seen in other studies (James et al. 1999; Landsberg et al. 1999b). However, Landsberg et al. (1999a) note the general absence of clear patterns and pointed to the complexity of grazing effects (such as strength of selection, degree of defoliation, and variance in recruitment opportunities) and lack of evolutionary history of grazing by large mammalian herbivores in Australia as reasons for weak selective pressure for grazing-related traits (Landsberg et al. 1999a).

Contrary to the observations in Australia mentioned in the previous paragraph, in arid Tunisian rangelands (mean annual rainfall = 100–200 mm), Jauffret and Lavorel (2003) found no decrease in the abundance of perennial grasses. This result is also in contrast with the observations in more mesic systems (Noy-Meir et al. 1989; Skarpe 1990; McIntyre and Lavorel 2001). Jauffret and Lavorel (2003) account for this due to the near or complete elimination of perennial grasses (e.g. *Pennisetum elatum* and *Hyparrhenia hirta*) and ascribed this to thousands of years of heavy grazing. This heavy grazing has left Tunisian ecosystems with a homogenized flora consisting only of species that are highly tolerant of herbivory and other forms of disturbance. Very similar results were obtained by Milchunas and Lauenroth (1993), as mentioned earlier.

A relative increase in woody shrubs has often been recorded in semi-arid rangelands, especially when these have a short- or light-grazing history (Archer et al. 1988; Pickup and Stafford Smith 1993; Skarpe 2000; Ward et al. 2004; Ward 2005b; Kraaij and Ward 2006). Chamaephytes (shrubs with below-ground growth structures) can resist intense or frequent disturbances by growing less tall and resprouting, and they tend to be less palatable than most grasses. The Tunisian system has apparently reached the stage where chamaephytes are the only life form remaining at abundances high enough to observe a significant response in terms of abundance and quality (also true in the Negev Desert in Israel; Ward and Olsvig-Whittaker 1993).

It has been reported in many arid ecosystems that annual species replace perennials following heavy grazing, owing to their ability to quickly invade open spaces and utilize soil resources (Kelly and Walker 1977; Cheal 1993; Freeman and Emlen 1995). Perennials are always present and thus are permanently available to browsers. The transient nature of the annual lifestyle means that herbivores are less likely to encounter them and, thus, they increase in abundance while perennials decrease with grazing. However, in a study of permanent plots from 1989 to 1996 in Namaqualand, South Africa (mean annual rainfall = 76 mm), Milton and Dean (2000) found that the reduction of perennial grasses by cattle grazing favoured annual plants in wet years only. Dry conditions prohibited the establishment of annual plants regardless of whether perennial grasses were present. This pattern has also been reported by Van Rooyen et al. (1991) and Jeltsch et al. (1997) in the Kalahari Desert, South Africa. Similarly, in a long-term study in a Chihuahuan Desert site in southeastern Arizona (North America), Kelt and Valone (1995) found that the removal of herbivores (cattle) had little impact on the abundance and diversity of annual plants. Historical effects of herbivory may cloud our ability to detect differences in the effects of herbivory on perennial and annual plants.

Palatability was a major factor for determining plant selection by herbivores in arid rangelands, according to the observations of Jauffret and Lavorel (2003) in Tunisia, Ward et al. (2000a) in Israel and Landsberg et al. (1999a) in Australia. Spiny plants were more frequent among grazing increasers in Tunisia. However, other studies have shown that spiny species such as *Echinops polyceras* and *Acacia raddiana* are favoured food plants of wild asses and camels, respectively (Rohner and Ward 1997; Ward et al. 1998). Some examples of reduced palatability are pertinent here:

1. Milton (1991) has shown that spinescence in plants increases with aridity, soil fertility, and mammalian herbivory at regional and local scales in the arid Karoo

of southern Africa. Vegetation of moist, nutrient-rich habitats within arid areas was more spinescent than that of the surrounding dry plains. Spinescence in plants of drainage lines and pans in arid southern Africa occurs in a wide range of genera and appears to have been selected by the effect of large mammals which concentrate on these moist patches. Milton (1991) concluded that, in arid areas, moisture may be important in mediating mammalian selection of spinescence.

2. Rohner and Ward (1997) have shown that there are inducible defences in *Acacia raddiana* trees in the Negev Desert of Israel because they only invest in a change of strategy when there is herbivory. In plants that are eaten, there are higher levels of condensed tannins in plants, leaves are smaller, and thorns longer (Fig. 7.5). Essentially, the thorns are hiding small leaves. Having small leaves is not a constraint because light levels are very high in deserts. However, in the absence of herbivory, larger leaves are the default condition because plants can grow faster when their light-capturing surfaces are larger. Ward et al. (2000a) and Jauffret and Lavorel (2003), among others, have shown that palatability (or lack thereof) may play an important role in determining the effects of mammalian herbivory on arid ecosystems. Jauffret and Lavorel (2003) found that long-spined species (such as *Astragalus armatus*) and *toxic* and *highly fibrous* species (such as *Thymelaea hirsuta*) are dominant in arid Tunisian rangelands as a consequence of the long grazing history. Similarly, unpalatable shrubs such as *Hammada scoparia, Thymelaea hirsuta*, and *Anabasis articulata* are often dominant in heavily grazed arid regions of the Middle East (Ward et al. 2000b; Ward 2005a). Geophytes, such as *Urginea maritima*, are also widespread and abundant in the Middle East, particularly where there is heavy grazing and trampling (Hadar et al. 1999). Similar to prostrate and rosette plants, they are close to or under the ground and unavailable to grazers for much of the year. When they produce leaves in the winter months, they are largely untouched by grazers because of the defensive chemicals in the leaves (Ward et al. 1997). Furthermore, the short reproductive

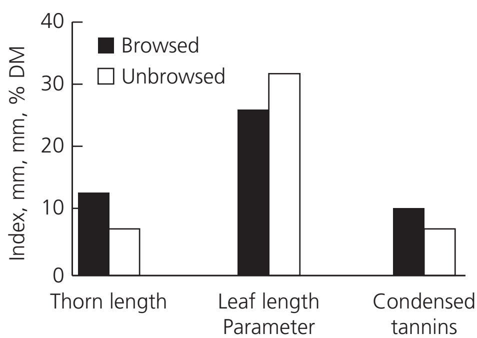

Fig. 7.5 *Acacia raddiana* leaves, tannins, and thorns. This species invests in higher tannin concentrations and hides its small leaves among long thorns.

Source: Modified from Rohner and Ward (1997). With kind permission of Opulus Press.

period of geophytes enables early flowering, seed setting, and dispersal despite heavy grazing (Hadar et al. 1999). However, Estell et al. (2014) found that there were declining levels of terpenoids protecting the one-seed juniper *Juniperus monosperma* in the Chihuahuan Desert with increased levels of herbivory, suggesting that this juniper was not well protected as herbivory increased. Such a decline in terpenoids could be explained by a trade-off with growth and/or reproduction.

3. Several recent studies have found that alkaloids in the columnar cactus *Trichocereus terscheckii* from the Monte Desert in Argentina can be toxic to the larvae of cactophilic fruit fly *Drosophila buzzatii* (Hasson et al. 2009; Padro and Soto 2013; Carreira et al. 2014). Padro et al. (2014) wished to test whether alkaloids would impose a stress during metamorphosis (i.e. on the larval stage) that had measurable morphological consequences on the adults. They increased the doses of these host plant alkaloids (mainly mescaline, N-dimethylmescaline, and α-methylmescaline) to *Drosophila buzzatii*. They tested the effects on the wing venation of the adult flies. Waddington (1939) had previously shown that changes in temperatures caused an epigenetic effect in development of *Drosophila*. Waddington (1939) called this *epigenetics* because it affected the later developmental stage of the organism. Another means of detecting such stress in an organism is to assess the degree of fluctuating asymmetry (FA) in bilateral asymmetry (Palmer and Strobeck 1986; Markow 1995). FA responds to within-individual bilateral variation caused by random perturbations accumulated during development (Palmer and Strobeck 1986; Parsons 1992). Padro et al. (2014) also examined whether alkaloids affected fluctuating asymmetry (Parsons 1990), another measure of epigenetic stress, in which the normal bilateral symmetry is distorted in some way. Padro et al. (2014) found that there was a change in the wing veins (Fig. 7.6) and in fluctuating asymmetry, as well as a change in wing size. They concluded that alkaloids caused the development of stress-response mechanisms in *Drosophila buzzatii*.
4. Plant secondary metabolites (PSMs) may act as defensive chemicals in fruits. This may deter potential seed predators. However, this may also deter seed dispersers. Cipollini and Levey (1997) developed the directed deterrence hypothesis (also known as the directed toxicity hypothesis) to explain how seed predators may be prevented from consuming fruits and seed dispersers attracted so as to disperse the fruits. Jordt and Julius (2002) have shown that rodent predators may be deterred from fruits and bird dispersers attracted to fruits based on differences in their sensitivity to capsaicin (the 'hot' compound in chili peppers). Capsaicin and other pungent vanilloid compounds cause a feeling of burning and tingling pain by activating a non-selective cation channel, called VR1, on sensory nerve endings. However, in chickens, the avian channel fails to be activated by capsaicin despite its general role as a multifunctional integrator for noxious stimuli. However, this differentiation was previously only known at the higher-taxon level, i.e. between birds and mammals (Jordt and Julius 2002). Samuni-Blank et al. (2012) have found that PSMs called glucosinolates in *Ochradenus baccatus*

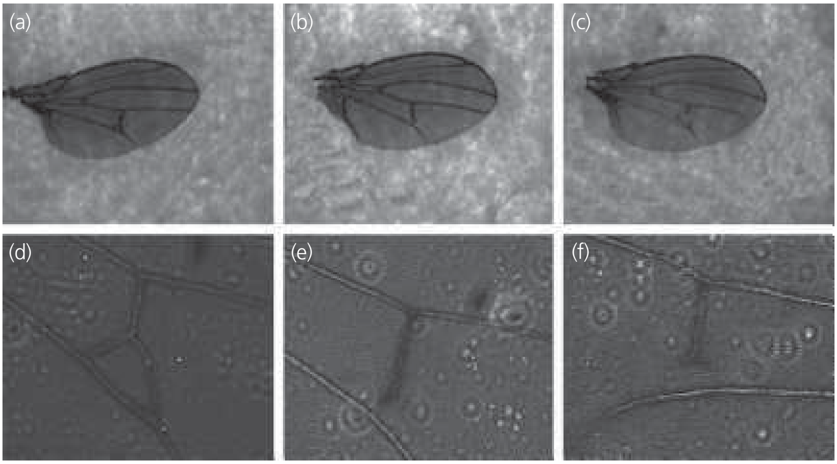

Fig. 7.6 Types of anomalies in the wing venation pattern involving the posterior cross-vein found in *Drosophila buzzatii* flies reared in vials with increased alkaloid concentrations. (a) Bifurcation of the posterior cross-vein (PCV); (b) nonjunction of the PCV and the longitudinal vein (L5); and (c) a combination of both anomalies in the same wing. (d–f) Magnification of the affected area of each anomaly type.

Source: Photo by J. Padro.

also deter the rodents *Acomys cahirinus* and *Sekeetamys calurus*. Intact glucosinolates are usually harmless but when plant tissue is damaged (as occurs during consumption), released myrosinases are hydrolysed to form thiocyanates, isothiocyanates, and nitriles, forming what is known as a 'mustard oil bomb' (Bednarek and Osbourn 2009; Winde and Wittstock 2011). These compounds are toxic to both *Acomys caharinus* (Fig. 7.7) and *Sekeetamys calurus* and are promptly spat out. In doing so, these rodents were acting as seed dispersers. When the mustard oil bomb was disarmed by inactivation of the myrosinase enzyme, one of the rodents, *Acomys cahirinus*, returned to its typical behaviour as a seed predator.

7.1.4 Is Australia a special case?—a meta-analysis

Vesk et al. (2004) performed a meta-analysis of 11 lists of grazing responses from five published Australian semi-arid and arid shrubland and woodland studies in an attempt to assess the generality of the results of the Diaz et al. (2001) study mentioned earlier. They found that the traits shown to predict grazing responses in the Argentinian and Israeli studies did not adequately explain responses in Australian semi-arid and arid rangelands. They found no effects of plant height or leaf size on grazing. Annuals were no less likely than perennials to decrease with increased grazing pressure (see also Milton and Dean 2000). Analyses of traits within growth forms provided little evidence for relationships between traits and responses other

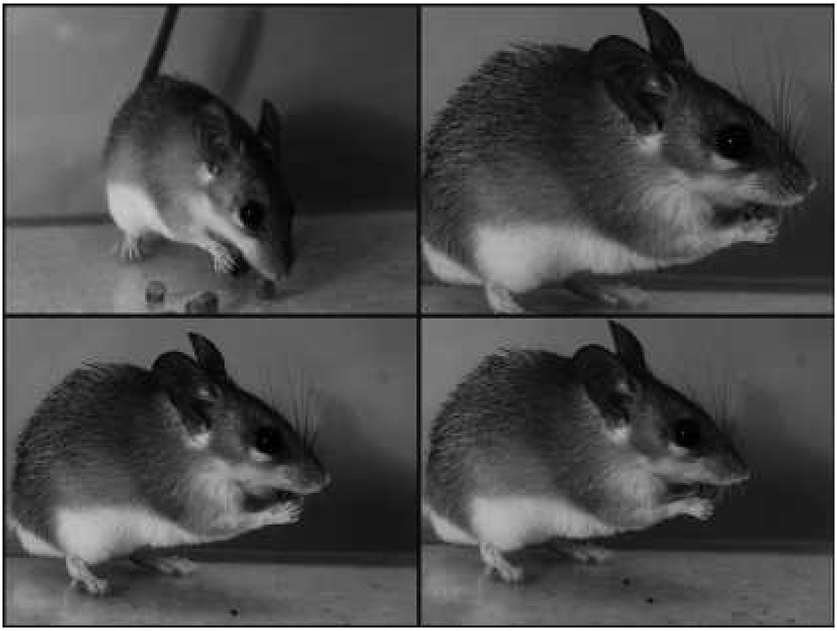

Fig. 7.7 Spiny mouse, *Acomys caharinus*, spitting out seeds of *Ochradenus baccatus*. The spiny mouse from the Negev Desert starts eating berries from the shrub (upper left). It soon spits seeds into its paws (upper right) and onto the ground (lower right and lower left). If the seeds were chewed at the same time as the fruit pulp, toxic chemicals would be hydrolysed. The plant has effectively turned the mouse from a seed predator into a seed disperser to help the plant reproduce.

Source: Photo by Michal Samuni-Blank.

than that annual grasses, which have high specific leaf area, tend to be increasers. Vesk et al. (2004) believe that because the Australian rangelands have lower productivity, less continuous sward, higher growth form diversity, and more bare ground than ecosystems in the Diaz et al. (2001) study, grazers can move through vegetation and taller species do not necessarily receive more grazing pressure because grazers can access short species from the side rather than by grazing the sward down to them. In contrast with Vesk et al.'s (2004) general conclusions, an earlier study of two arid Australian shrublands (which was included in the meta-analysis of Vesk et al. (2004)) found associations between increased grazing pressure and small plant size, small leaves, high fecundity, and plasticity of growth form (Landsberg et al. 1999a). However, many attributes of plants recorded in the Landsberg et al. (1999a) study varied independently of each other and grazing-related attributes were only convincingly demonstrated in grasses. Vesk et al. (2004) recognized that they could not discount evolutionary history of grazing or the 'Australia is a "special case" argument' for the differences between their results and those of Diaz et al. (2001).

7.1.5 Effects of insect herbivory on desert plants

Crawley (1989) claimed that plants have more impact on the population dynamics of insects than insects have on the population dynamics of plants. In general, it is probably true that monophagous desert insects have little impact on equilibrium plant abundance even when the insects are food-limited (Crawley 1983). However, several studies have suggested that herbivorous insects have a great impact on the evolution and population dynamics of desert plants (Ayal and Izhaki 1993; Ayal 1994; Becerra 1994; Wilby et al. 2005). Herbivorous insects may reduce the reproductive success of their host plants either by directly feeding on their flowers (Ayal and Izhaki 1993; Ayal 1994) and seeds (Wilby et al. 2001; Or and Ward 2003) or by indirectly feeding on other plant parts such as foliage and roots (Becerra and Venable 1990; Becerra 1994).

Three examples where insects have notable interactions with desert plants are described in the following.

7.1.5.1 Mirid bug (Capsodes infuscatus)

Ayal and Izhaki (1993) and Ayal (1994) have studied the mirid bug, *Capsodes infuscatus* (Hemiptera: Miridae), in a central Negev Desert habitat in Israel. This bug deposits eggs inside the inflorescence stalk of its host plant *Asphodelus ramosus* (Fig. 7.8) in spring. Developing nymphs as well as adults feed on this plant. Different structures of *Asphodelus ramosus* are consumed by the bugs, including leaves, flower stalks, buds, flowers, and fruits (Ayal and Izhaki 1993). *Capsodes infuscatus* nymph feeding may kill young inflorescences or suppress the development of the inflorescence branches and kill all its flowers while adult feeding may also kill green fruits (Ayal 1994). All stages of *Capsodes infuscatus* feed upon *Asphodelus ramosus*. Nymphs consume leaves early in the season, but as they develop, they feed on inflorescence stalks, flowers, and fruits (Ayal and Izhaki 1993). A positive correlation between the number of young nymphs of *Capsodes infuscatus* per clone (*Asphodelus ramosus* also reproduces vegetatively) early in the season, long before fruit appearance, and consequent

Fig. 7.8 *Asphodelus ramosus* from the Negev Desert.

damage to fruit production in *Asphodelus ramosus* has been shown (Ayal and Izhaki 1993).

*7.1.5.2 Leaf beetle (*Blepharida *sp. nov.)*

One example of an interesting chemical interaction in desert ecosystems is between a tree (Family: Burseraceae) and a leaf beetle (Family: Chrysomelidae). A desert tree from Tehuacan Desert near Zapotitlan, Mexico, *Bursera schlechtendalii*, has resinous ducts in its leaves that eject an unpleasant syringe-like squirt of terpene resins, from 5 to 150 cm and may persist for a few seconds (Fig. 7.9). Some leaves do not actually squirt liquid into the air but still release large amounts of terpenes that cover the surface of the leaf (called the 'rapid bath response' by Becerra and Venable (1990)). The leaf beetle *Blepharida* sp. nov. is capable of severing the resin canals by biting the midvein of the leaf (Becerra 1994). Becerra (1994) determined the reaction of larvae to *Bursera* resins by allowing them to incise the leaf midveins and then moving them to intact leaves. Canals were intact in the new leaves, leaving the beetle larvae with a squirt of resins. They attempted to clean themselves and then abandoned the leaf. The larvae may even remain inactive for several hours before starting to incise another leaf. Thus, resin flow can deter this beetle if canals are not deactivated (Becerra and Venable 1990). Larvae living on plants with a higher frequency of leaf response had greater mortality or, in some cases, were smaller. Early instar larvae are incapable of severing leaf veins because of their smaller mandibles. They feed by mining the surfaces of the leaves but sometimes die when they rupture the resin canals (Becerra 1994).

Interestingly, larvae from low-response plants increased the time that they took to cut the veins of *Bursera* when transplanted to high-response plants. When placed on high-response plants, some larvae fed without cutting the veins and were covered with resins. After getting squirted by several leaves, they started to sever the leaves. Larvae from high-response plants continued cutting veins after being deposited on

Fig. 7.9 Forceful squirt from *Bursera* sp.

Source: From Becerra (1994). With kind permission of the Ecological Society of America.

less responsive plants although they did so for a shorter time. These differences in behaviour based on their experiences on previous plants indicate that the behaviour is plastic and that *Blepharida* pays a handling-time cost. Becerra and Venable (1990) showed that *Blepharida* larvae can take up to 1.5 h to deactivate the resin canals of a single leaf of a high-response plant, yet consuming the leaf thereafter can take 10–20 min only.

*7.1.5.3 Insect interactions with cholla cactus (*Opuntia imbricata*)*

Miller et al. (2009) tested whether herbivory by four insect species could affect the dynamics and distribution of the tree cholla cactus (*Opuntia imbricata*), which is a long-lived perennial plant. They tested this across an elevational gradient in central New Mexico, U.S.A., in the Chihuahuan Desert. The four insect species were a sap-feeding cactus bug *Narnia pallidicornis*, a stem-boring cerambycid beetle *Moneilema appressum*, an unidentified weevil that feeds externally on vegetation and reproductive structures, and a predispersal seed predator *Cahella ponderosella*. These authors examined the relative effects of herbivory from low-elevation desert grassland (1670 m) to a grassland–mountain transition zone (1720 m) to the rocky slopes of the Los Pinos Mountains (1790 m). They found that tree cholla density increased significantly with elevation, while damage by these insects decreased.

Miller et al. (2009) reduced the degree of insect herbivory across this elevational gradient. They found that the effects of insect exclusion on plant growth and seed production were strongest in the low-elevation grassland and decreased in magnitude with increasing elevation (Fig. 7.10). The total effect of insect herbivory on tree cholla population growth was due to a combination of reductions in plant growth and in fecundity. They found that the relative contribution of each of these effects varied according to the position on the elevational gradient. Interestingly, Miller et al. (2009) ascribe this spatial variation to the differential effects of an ant–plant mutualism. The tree cholla secretes extrafloral nectar and is tended by two ant species, *Crematogaster opuntiae* and *Liometopum apiculatum*. Ants gain from the extrafloral nectar provided by the host plant. *Liometopum* is an effective ant guard against cactus-feeding insects, such as those described earlier. Contrastingly, *Crematogaster* is an ineffective ant guard. *Liometopum* is much more common at high altitudes and *Crematogaster* is more common at low altitudes. Miller et al. (2009) hypothesize that strong defence by the effective ant guard restricts insect herbivores at high elevations, which consequently affects the density of the tree cholla on this gradient.

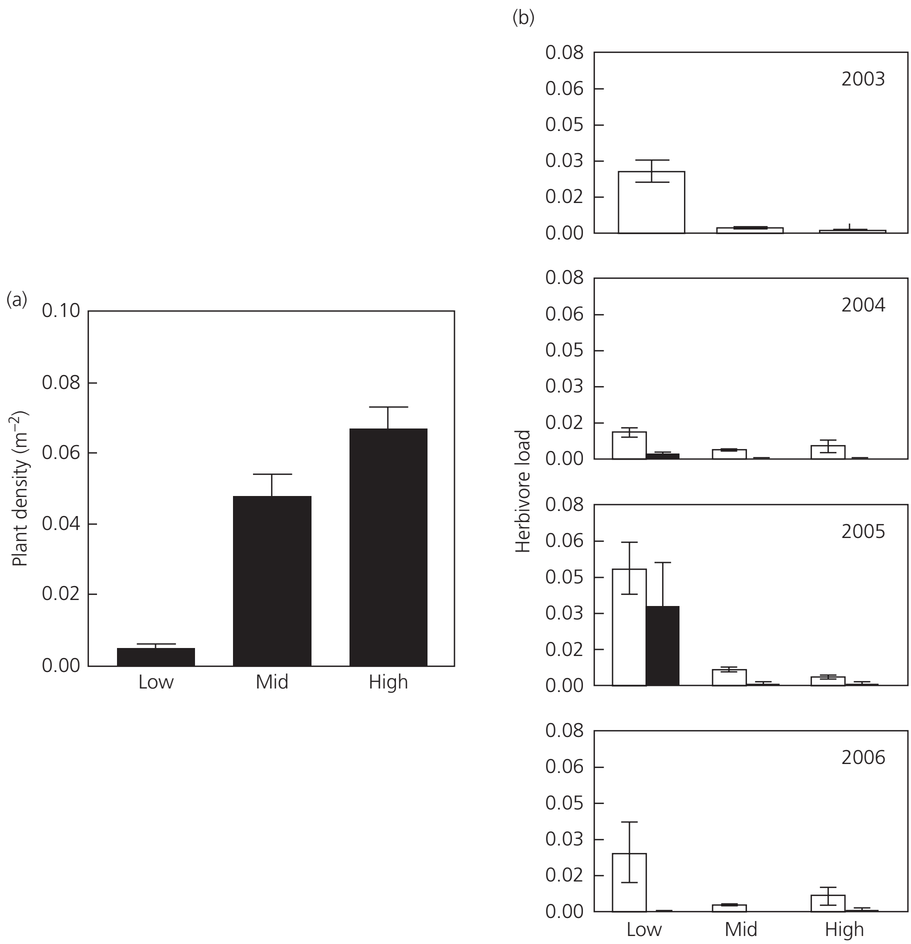

Fig. 7.10 Changes in tree cholla cactus density and herbivore load with elevation in the Chihuahuan Desert in central New Mexico, U.S.A. (a) Density of tree cholla cactus (expressed as number/m^2), and (b) insect herbivore load (measured as insect mass/plant resource structure).

Source: From Miller et al. (2009). With permission of the Ecological Society of America.

7.2 Pollination

The most frequent type of mutualism is plant–pollinator interactions (Stiling 2010). Facultative mutualisms allow for co-pollination (by several pollinators), whereas obligate mutualisms involve the complete interdependency of both partners, the best-known example of which is the fig–fig wasp system (Bronstein 2001). The interactions between yuccas and yucca moths and senita cactus and senita moths are obligate mutualisms that naturally occur in deserts (Fig. 7.11).

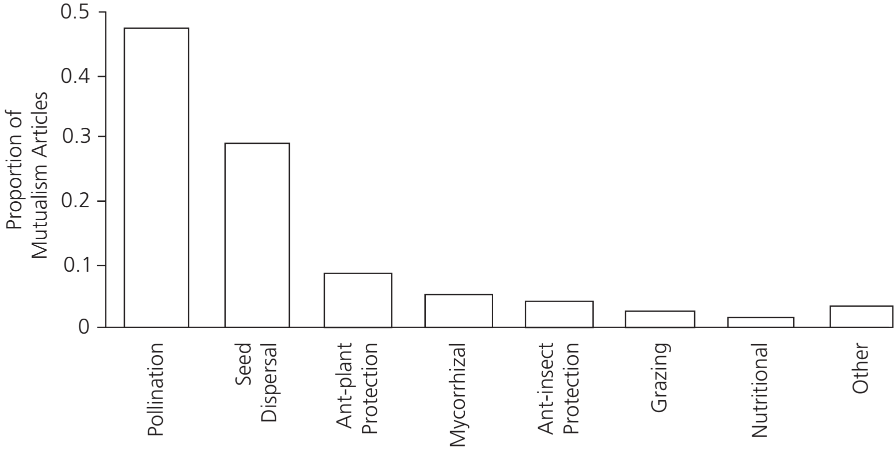

Fig. 7.11 Frequency of different types of plant–animal interactions listed as mutualisms, based on the number of articles published on a particular topic.

Source: From Stiling (2002). With kind permission of Pearson Higher Education Company.

Waser et al. (1996) expect plant generalization (i.e. more than one pollinator per plant species) to occur as long as temporal and spatial variance in pollinator quality is appreciable, different pollinator species do not fluctuate in unison, and they are similar in their pollination effectiveness. Further, they consider pollinator generalization likely to occur when floral rewards are similar across plant species, travel is costly, constraints of behaviour and morphology are minor, and/or pollinator lifespan is long relative to flowering of individual plant species. Nevertheless, plants with highly specialized pollination systems are not uncommon in the tropics and some temperate regions (reviewed by Johnson and Steiner 2000).

One of the more interesting examples of pollinator specialization and diversification occurs in the guild of bees that pollinate the creosote bush *Larrea tridentata*. In this case, the historical biogeography (20,000 years BP to the present) of this desert plant is well understood (Minckley et al. 2000). This history, coupled with the distribution pattern of its bee fauna, suggests that the specialization for creosote bush pollen has evolved repeatedly among bees in the Lower Sonoran and Mojave deserts. In these highly xeric environments, species of specialist bees surpass generalist bees in diversity, biomass, and abundance (Minckley et al. 2000). These specialist bees can facultatively remain in diapause through resource-poor years and later emerge synchronously when their host plants bloom in resource-rich years. Repeated origins of pollen specialization to one host plant where flowering occurs least predictably is a counterexample to Waser et al.'s (1996) proposition. Host–plant synchronization, perhaps a paucity of alternative floral hosts, or even the flowering attributes of creosote bush or a combination of these factors may account for the diversity of bee specialists that depend on *Larrea tridentata*.

7.2.1 Yucca–yucca moth mutualism

Yucca plants (genus *Yucca*) and yucca moths (genera *Tegeticula* and *Parategeticula*; Lepidoptera, Family: Prodoxidae) are highly coevolved. Particular species of moth have evolved with particular species of yucca. The pollinator of the yucca is always female. While at the flower, the moth climbs halfway up the pistil and inserts her ovipositor into the ovary of the plant (Fig. 7.12). The moth's eggs are laid into the plant's ovary. She then climbs up to the top of the pistil and rubs some of her collected pollen onto the stigma of the plant, fertilizing the flower, and thereby ensuring the production of seeds (Miller 1995). As the larvae develop, they feed on the developing seeds of the yucca, but they only eat a portion of them. What is different about this relationship is that there is no immediate reward for the individual insect following the pollination process (Pellmyr 2003). In more conventional plant–pollinator interactions, the pollinator will be rewarded with nectar and pollen, which happens to fertilize the next plant visited. Here, the yucca moth collects pollen, although she does not eat it. Pellmyr's (2003) theory about the costs of seed production and the natural selection of *Tegeticula* and *Parategeticula* moths holds that if the moths lay a greater number of eggs, then the plant would suffer because of the moth's reproductive success (i.e. the larvae would eat almost all the fertilized seeds of the plant). Evolutionarily speaking, moths that lay too many eggs and, thus, minimize the production of the developing seeds are disadvantaged because the flower in question aborts the developing fruit and the larvae relying on it starve. This keeps the moth–yucca equilibrium stable, so the fitness increases in one species do not affect those of the other.

Fig. 7.12 Head of female yucca moth, *Tegeticula carnerosanella*, with yucca pollen load. Black arrow = left tentacle; white arrow = proboscis.

Source: From Pellmyr and Krenn (2002). With kind permission of National Academy of Sciences, USA.

When two organisms have evolved to a point where both benefit from the relationship and neither is harmed, mutualism occurs. Coevolution of stable mutualism occurs because both species have mechanisms to prevent excessive exploitation. For example, yucca flower abortion occurs if too many eggs are laid (Pellmyr and Huth 1994). A strong negative effect exists between moth egg number and probability of flower retention in yuccas. Furthermore (Pellmyr and Huth 1994) showed a strong positive effect between the number of pollinations received and the probability of flower retention. Selective maturation of fruit with low egg loads and high pollen loads provides a mechanism to increase the quantity and possibly the quality of seeds produced, and simultaneously select against moths that lay many eggs per flower or provide low-quality pollinations. These results explain the stability of this type of interaction and explain why selection for high-quality pollination also provides a mechanism to help explain the evolution of active pollination among yucca moths.

Is there also a genetic cost through selfish moth behaviour that may lead to high levels of self-fertilization in the yuccas? Observations of a *Tegeticula yuccasella* yucca moth on *Yucca filamentosa* revealed that females remained on the plant and oviposited in 66% of all instances after observed pollen collections, and 51% of all moths were observed to pollinate the same plant (Pellmyr et al. 1997). Manual cross-pollination and self-pollination showed equal development and retention of fruits. Subsequent trials to assess inbreeding depression revealed significant negative effects on seed weight and germination frequency in selfed progeny arrays. Cumulative inbreeding depression was about 0.48 (i.e. the fitness of selfed seeds was less than half that of outcrossed seeds; Pellmyr 1996). Estimates of outcrossing rates based on allozyme analyses of open-pollinated progeny arrays did not differ from 1.0; thus, outcrossing was the mode of reproduction. The discrepancy between high levels of behavioural self-pollination by the moths and nearly complete outcrossing in mature seeds can be explained through selective foreign pollen use by the females, or, more likely, pollen competition or selective abortion of self-pollinated flowers during early stages of fruit development. Thus, whenever the proportion of pollinated flowers exceeds the proportion that can be matured to ripe fruit based on resource availability, the potential detrimental genetic effects imposed through self-fertilized pollinations can be avoided in the plants. Because self-pollinated flowers have a lower probability of retention, selection should act on female moths to move among plants whenever moth density is high enough to trigger abortion.

Yucca moths are the only known pollinators of the yucca (O. Pellmyr, pers. comm.). Obviously, at the time of first colonization of the yuccas (yuccas are phylogenetically older than yucca moths), another pollination agent would have existed. The key is likely to be that pollination carries an unusually high fitness consequence in insects whose larvae are seed consumers. A female moth that can increase the probability of fruit production in flowers where she has laid eggs will have higher fitness than one who is less likely to do so, which can explain the origin and maintenance of active pollination in the moths. Can a moth stop pollinating if they select flowers that have already been pollinated? In at least some moth species, female moths can tell (by hormonal means) whether a flower has been visited before, and they are less likely to pollinate again (Pellmyr, pers. comm.). The drawback is that laying more eggs per flower (a consequence of coming second) reduces the probability of fruit retention quite dramatically, so there is a big fitness loss to investing only in previously visited flowers. Another important factor is that the fitness cost (in terms of structure and time allocation) of being a pollinator is trivial, so there is not a lot of selection against it (Pellmyr, pers. comm.).

Regarding cheating behaviour, Addicott and Tyre (1995) consider there to be partial support for the flower-dependent behaviour and probabilistic behaviour hypotheses for cheating in the yucca moth, *Tegeticula yuccasella*, and the yucca, *Yucca kanabensis*. The flower-dependent hypothesis predicts that moths will respond to previous visits to a flower by modifying their oviposition and pollination behaviour. These flowers may have received sufficient pollen for complete fertilization of their ovules and, therefore, female yucca moths could conserve their pollen. This would allow them to have more pollen available to pollinate previously unvisited flowers without having to collect more pollen and move to another inflorescence. This hypothesis depends on the assumption that yucca moths are able to detect the presence of previous ovipositions and that ovipositions are a good predictor of pollen in the stigma. Addicott and Tyre (1995) do not think that yucca moths detect pollen in the stigma because they only approach the stigma for the purpose of pollination. As predicted by this hypothesis, yucca moths modified their behaviour on previously visited flowers because bouts on such flowers involved fewer ovipositions and either a lower proportion of ovipositions followed by pollination or no pollination. However, the hypothesis does not explain why some moths failed to attempt to pollinate flowers that had not been visited. Why would some moths not collect pollen or at least not collect pollen again once their initial supply is exhausted? According to Addicott and Tyre (1995), the most probable answer to this is that the moths are risk averse and the yuccas are self-incompatible. Moths that gather pollen from an inflorescence and then pollinate flowers on that inflorescence will experience very low reproductive success because the retention rate of self-pollinated flowers is basically zero (Pellmyr 1996). Moths that collect pollen should fly to another inflorescence but this may entail considerable risk, either due to predation by bats and night hawks (Aves: Caprimulgidae) or because they may struggle to find another inflorescence.

The second hypothesis addressed by Addicott and Tyre (1995), the probabilistic behaviour hypothesis, uses a mixed strategy in an evolutionarily stable strategy (ESS) model of game theory (Maynard Smith 1982), where moths might respond to the probability that a particular flower had been pollinated previously or would be visited subsequently and pollinated by at least one other moth. The probability of visitation would be a function of the density of moths relative to flowers, which could vary between years, study sites, or even within seasons (James et al. 1994). There is some support for both of Addicott and Tyre's (1995) hypotheses. They are not mutually exclusive because conditional mixed strategies are possible. The probability of pollination could depend on the state of the flower (e.g. number of previous ovipositions) and the state of the moth (e.g. age), as well as the density of moths relative to flowers, which would affect the probability of future visits by other moths to a certain flower (Parker 1984).

Cheater yucca moth species have evolved at least twice. Underlying obligate mutualism is an intrinsic conflict between the parties, in that each is under selection for increased exploitation of the other. Theoretical models suggest that this conflict is a source of evolutionary instability, and that evolution of 'cheating' by one party may lead to reciprocal extinction. Pellmyr et al. (1996) present phylogenetic evidence for the reversal of an obligate mutualism: within the yucca moth complex, distinct cheater species derived from obligate pollinators inflict a heavy cost on their yucca hosts. Phylogenetic data show the cheaters to have existed for a long time. Coexisting pollinators and cheaters are not sister taxa, supporting predictions that the evolution of cheating within a single pollinator is evolutionarily unstable. Several lines of evidence support a hypothesis that host shifts preceded the reversal of obligate mutualism. Host or partner shifts are mechanisms that can provide a route of evolutionary escape among obligate mutualists in general.

In another study, Marr et al. (2001) have focused on interactions between a cheater moth, *Tegeticula intermedia*, and the pollinator *Tegeticula yuccasella* in fruits of the host plant *Yucca filamentosa*. They examined the effects of larval competition on the two species of moth. They found it to be weak and asymmetric, affecting the cheater larvae to a greater extent. There were insufficient larvae to cause seed limitation because no effect of pollinator larvae on either mass or mortality of cheater larvae was detected in years with the highest larval densities per fruit (yuccas abort fruits with many yucca moth larvae). This result is consistent with the hypothesis that the recent rapid radiation of species in the *Tegeticula yuccasella* complex (there is more than one species in this group) may be explained by the ability of multiple pollinator species (some of whom have become cheaters) to use fruits without severe competition. Pellmyr (pers. comm.) considers this to have been preceded by host shifts that led to the coexistence of two pollinator species on a host. In such circumstances, loss of pollination can occur whether there is a fitness cost or not and becoming a cheater may not be selected for at all. Rather, there is a temporal niche shift that permits the cheater species to exploit seed resources that cannot be accessed by pollinator larvae. Therefore, there is no evidence for the selection for cheating per se, but it occurs merely as a by-product of another driver, namely, lack of access to the yucca seeds by the pollinator larvae.

7.2.2 The senita cactus–senita moth obligate mutualism

The senita moth, *Upiga virescens* (Pyralidae, Lepidoptera), and the senita cactus, *Lophocereus schottii*, occur in the Sonoran Desert in the U.S.A. and Mexico and are mostly obligate mutualists (see end of this paragraph; Fig. 7.13). The senita moth, similar to the yucca moth, has specialized morphological features that allow for pollen loading. Similar to other Lepidoptera, female senita moths avoided ovipositing eggs in flowers that contained an egg. Eggs hatch within three days of flower closing and larvae crawl down

Fig. 7.13 Senita moths on senita cactus.
Source: Copyright of Greg and Mary Beth Dimijian.

the wilting corolla and bore into the top of the fruit, which they consume before entering the cactus branch to pupate. However, only a fraction of eggs produced larvae that survived to become seed consumers themselves. About 20% of fruits were destroyed by larvae. Benefits of senita moths to pollination and fruit set in the senita cactus were about three to four times the costs of seed mortality induced by the larvae, which is similar to the yucca mutualism (Addicott and Tyre 1995). Although co-pollinators are absent in yucca mutualisms, Fleming and Holland (1998) have shown that diurnal halictid bees may also pollinate senita flowers. However, temperature-dependent flower closing limits their effectiveness (flowers are only open for a few hours in the day, usually when it is overcast). Nonetheless, the senita cactus is not entirely dependent on the senita moth and, consequently, lies between the categories of obligate and facultative mutualist. Reduction in and lack of nectar production in the senita cactus discourage co-pollinators that visit flowers for nectar rewards only. Reduced nectar production clearly conserves energy for use in fruit production where fruit set is resource-limited.

For senita cactus and senita moth interactions, it is the great benefit to plants from pollination by moths and the low survivorship of moth larvae that maintain the high benefit-to-cost ratio of the plant. Selective abortion of fruit in yucca appears to be a mechanism inhibiting overexploitation by yucca moths (Pellmyr and Huth 1994), but senita fruits contain only one larva each (no continuum occurs as in yucca fruit). Thus, the criterion for abortion would have to be presence or absence of larva in a fruit. Holland and Fleming (1999) assume that, where resources limit fruit production, flowers with greater pollination quality and quantity would be preferentially retained by plants, increasing progeny survival of moths that actively pollinate.

There is a major cost associated with a mutualistic relationship, such as the yucca moth–yucca or senita moth–senita cactus relationship. If either of the species, for any reason, cannot be found at the right place at the right time, each of the species suffers reproductive failure. Bronstein (2001) found that, if yuccas bloomed late, they ended up out of synchrony with the emergence of most yucca moths. As a result, the yucca fruits which set seed were the very earliest ones; late-blooming plants failed completely. This dependence on timing, which only spans approximately a month in the case of yucca, can easily contribute to reproductive failure in both species. In the case of senita cactus, prolonged flowering occurs, which reduces the possibility of reproductive failure for the senita moth.

7.3 Seed dispersal and seed predation

The effects of seed predators, such as desert rodents, finches, sparrows, and harvester ants, are less dramatic but may be equally effective at controlling plant populations. For example, Brown and Heske (1990) removed three species of kangaroo rats (*Dipodomys* spp.) from plots of Chihuahuan Desert shrub habitat from 1977 to 1990 and found that the density of tall perennial and annual grasses had increased approximately threefold and rodent species typical of arid grassland had colonized. In the same study, Heske et al. (1993) showed that significant increases in the abundance of a tall annual grass (*Aristida adscensionis*) and a perennial bunch grass (*Eragrostis lehmanniana*) occurred. This change in vegetative cover affected the use of these plots by several other rodent species and by foraging birds. The mechanism producing this change probably involved a combination of decreased soil disturbance and reduced predation on large-sized seeds when kangaroo rats were absent. Species diversity of summer annual dicotyledonous plants was greater on plots where kangaroo rats were present, as predicted by keystone predator models (Fig. 7.14). However, Heske

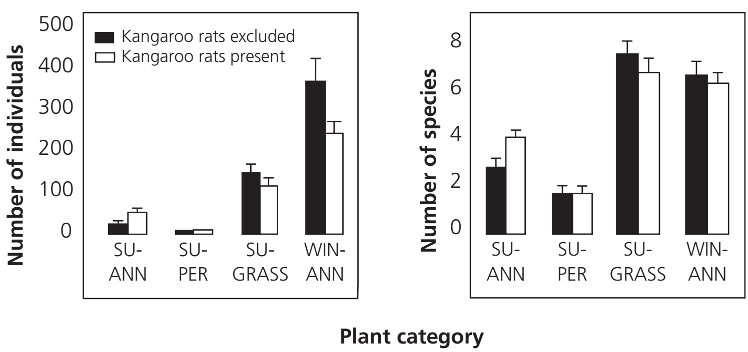

Fig. 7.14 There were significant increases in the abundance of a tall annual grass (*Aristida adscensionis*) and a perennial bunch grass (*Eragrostis lehmanniana*) as a result of kangaroo rat exclusion. Differences in plant species diversity were found for summer annual dicot species only. SU = summer, WIN = winter, ANN = annual, GRASS = grasses, and PER = perennial. Bars = S.E.

Source: From Heske et al. (1993). With kind permission of Springer.

et al. (1993) were unclear whether this was caused directly by activities of the kangaroo rats or indirectly as a consequence of the increase in grass cover. Their study site was located in a natural transition between desert scrub and grassland, where abiotic conditions and the effects of organisms may be particularly influential in determining the structure and composition of vegetation. Under these conditions, kangaroo rats may have a dramatic effect on plant cover and species composition.

Seed dispersal by large mammalian herbivores is also important, particularly in cases where the seeds are hard (see Campos and Ojeda (1997) with regard to *Prosopis*, Rohner and Ward (1999) with regard to *Acacia*). In many cases, germination of seeds (such as of *Acacia* species) increases as mammal body size increases (see Fig. 11.4). This is because the mammals ingest the seeds and defaecate them later. This scarifies the seed and the greater the body mass of the animal, the longer it remains in the gut and the greater the mechanical effect of the gut's hydrochloric acid on inducing scarification (Rohner and Ward 1999; Bodmer and Ward 2006). In *Acacia* species, the seeds are very hard and can only germinate once scarification occurs. This may be done by water, requiring waiting until the rains in the following year, or they can be dispersed by large mammals. In some cases, there can be negative effects on germination, such as in ostrich, *Struthio camelus* (Aves, Family: Ratites), in Israel (Rohner and Ward 1999) and wild boar, *Sus scrofa*, in the Monte Desert in Argentina (Campos and Ojeda 1997). In these cases, all seeds are damaged and cannot germinate.

In a 17-year study in the central Negev Desert highlands of Israel, Indian crested porcupines, *Hystrix indica*, were found to focus their activities in midslope areas where plant biomass was maximal due to run-off water accumulation (Shachak et al. 1991; Boeken et al. 1995). In a 5-year study of a population of *Tulipa systola* in the same desert highlands, herbivory by porcupines was generally low although the effects on recruitment were consistently greater than on other parts of the life history (Boeken 1989), but they do not generally limit geophyte populations. However, pits dug by porcupines accumulate organic material, including seeds and water (Gutterman and Herr 1981; Boeken and Shachak 1998; Boeken et al. 1998). As a result of this accumulation of materials, plant density, biomass, and species richness were found to be much higher in porcupine diggings than in undisturbed areas (Boeken et al. 1995). These authors showed that plant density and diversity were limited by microsite availability due to a lack of water infiltration in undisturbed areas (Fig. 7.15). In contrast, diggings remained moist throughout the growing season and diggings were only limited by seed arrival.

Granivory is an important interaction in ecological communities, especially in deserts where many plant populations exist as seeds for long periods (Davidson and Morton 1981; Morton 1985; Rissing 1986). Granivores can also be seed dispersers. Harvester ants have been shown, in a number of deserts (Australia, South Africa, and South America), to be the most important granivores and seed dispersers (Morton 1985; Kerley 1991) (Fig. 7.16), although rodents are more important in North American and Israeli deserts (Mares and Rosenzweig 1978; Abramsky 1983).

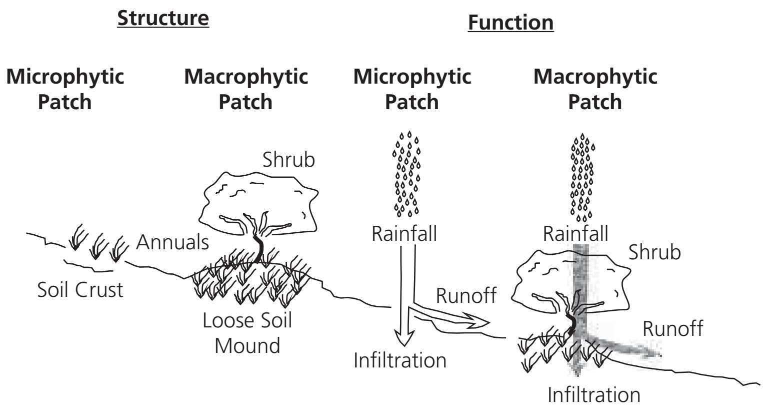

Fig. 7.15 Side view of a hill slope showing importance of porcupine diggings to plant diversity.
Source: From Boeken et al. (1995). With kind permission of Wiley-Blackwell.

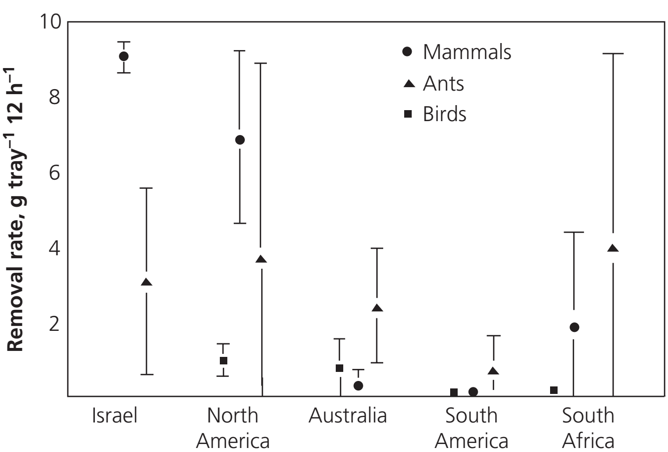

Fig. 7.16 Comparison of effects of ants, small mammals, and birds across several continents.
Source: From Kerley (1991). With kind permission of Elsevier.

7.3.1 Myrmecochory

Myrmecochory, or seed dispersal by ants, is often regarded as a diffuse mutualism between a guild of plants and a guild of ants (Hughes and Westoby 1992; Giladi 2006). This phenomenon has been reported in over 3000 plant species and in more than 80 plant families, in many different ecosystems. Many seeds have appendages, known as elaiosomes, which are lipid-filled structures that are attractive to ants and encourage dispersal to 'safe sites' for germination and growth (Rissing 1986). Elaiosomes are not as common in deserts as in more mesic ecosystems but there are other structures used to attract ants to seeds (see the following).

Davidson and Morton (1981) have recorded myrmecochory in a wide range of Australian species, especially in diaspores of the family Chenopodiaceae. The widespread and dependable presence of ants in the Australian deserts, and the relative importance of ant species capable of carrying such large diaspores, lead to the dependence of Australian plants on these dispersal strategies.

Rissing (1986) found that six plant species were significantly associated with nests of the desert seed-harvester ants, *Veromessor pergandei* and *Pogonomyrmex rugosus*, in the Mojave Desert. Seeds of two common annuals, *Schismus arabicus* and *Plantago insularis*, have 15.6 and 6.5 times more fruits or seeds growing on ant nest refuse piles than nearby controls do. Interestingly, these two common annuals do not have obvious appendages such as elaiosomes that are attractive to ants.

Similar results have been recorded by Wilby et al. (2001) in the northern Negev Desert, Israel, for *Messor ebeninus* and *Messor arenarius*. A total of 55 plant species were found on the nest mounds as opposed to 25 in the undisturbed soil. The favoured food items of *Messor ebeninus* are seeds of the grass *Stipa capensis*. In contrast with other plant species *Stipa capensis* occurred at much lower densities on the nest mounds, probably reflecting consumption. Another common species, *Reboudia pinnata*, increased from about 10% of samples on the undisturbed soil to 85% of mound samples. This last-mentioned plant species has a hardened fruit wall, which protects the seeds from predation (Gutterman 1993).

There are a number of hypotheses for the evolution of myrmecochory (Giladi 2006). The main hypotheses are: (1) the directed dispersal hypothesis, which holds that ants displace seeds to sites where the plant fitness is higher than it would be in a random location, most likely due to nutrient enrichment at or near the ant nest (Hanzawa et al. 1988, Giladi 2006); (2) distance dispersal hypothesis, whereby seed dispersal reduces parent–offspring conflict and sibling competition; and (3) predation-avoidance hypothesis, whereby dispersal and burial of seeds by ants reduce the ability of seed predators to locate and obtain seeds. Beattie (1985) argued that the directed dispersal hypothesis was the best-supported hypothesis. This hypothesis is still perceived as the leading hypothesis on the evolution of myrmecochory (Wenny 2000), even though it has frequently been challenged (Bond et al. 1990; Westoby et al. 1991). In Giladi's (2006) later review, which included 62 studies, the directed dispersal hypothesis was supported in about half of the studies (12 of 26 = 41%) that tested it. Giladi (2006) considered that the predator-avoidance hypothesis (81% support) and the distance-dispersal hypothesis (76% support) were better supported.

Ant dispersal distances are typically short, on the order of 0.01–180 m (Gomez and Espadaler 2013), with a mean value of 2.24 ± 7.19 m ($n = 183$). An interesting example of long-distance dispersal by ants comes from meat ants, *Iridomyrmex viridiaeneus*, dispersing *Acacia ligulata* tree diaspores in arid Australia (Whitney 2002).

Iridomyrmex viridiaeneus moved diaspores between 7 and 180 m (mean approx. 94 m) from the source trees to their nests. These ants subsequently removed the arils underground and discarded the seeds over about 3000 m^2 from their nests. About 40% of the discarded *Acacia ligulata* seeds were viable, with about 80% in a dormant condition.

7.3.2 Diplochory: using two mechanisms to disperse

Vanderwall and Longland (2004) consider the situation where more than one mechanism of seed dispersal is used. They consider this to be an effective way of dispersing far (Fig. 7.17). Phase one involves dispersing away from the parent plant (and concomitant competition) and phase two involves moving seeds to safe sites where germination and survival probabilities are greater. Rickert and Fracchia (2010) consider the case of diplochory in the Monte Desert of Argentina in two species of *Jatropha* (Euphorbiaceae). These two species both use explosive dispersal to get away from the parent plant (phase one), followed by ant dispersal (phase two). They show that this second phase is not coincidental because both of these *Jatropha* species possess elaiosomes to attract ants to disperse them. The heavier seeds of *Jatropha hieronyma* (about 8 times heavier than *Jatropha excisa*) disperse considerably further than the other species, reaching a maximum of about 18 m. These authors found that seeds possessing elaiosomes were dispersed further than those where the elaiosomes were removed by the researchers. Despite the greater mass of *Jatropha hieronyma* and the consequent difficulty in handling the seeds that was experienced by ants, *Jatropha hieronyma* was dispersed further by ants than *Jatropha excisa*. The total distance

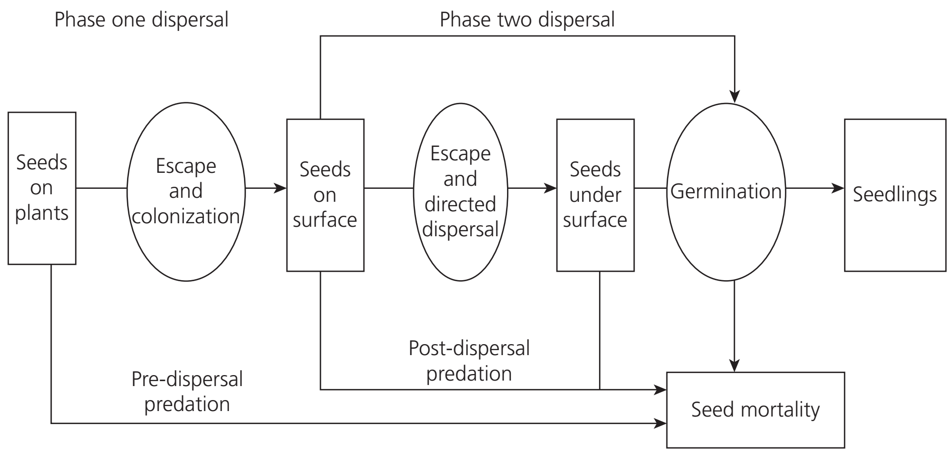

Fig. 7.17 Schematic diagram of the process of diplochory.

Source: From Vanderwall and Longland (2004). With kind permission of Cell Press.

moved was similar to that recorded for diplochory in other ecosystems (Vanderwall and Longland 2004).

7.4 Are these coevolved systems?

All mutualistic interactions can be viewed in terms of the Red Queen hypothesis (Van Valen 1977) because each mutualist needs to evolve continually to avoid being exploited by its mutualist partner. Thus, such highly coevolved systems arose despite the needs of each conflicting!

1. To the plant, an ideal pollinator or seed disperser would move quickly among individuals but retain high fidelity to a plant species so that little pollen or seed is wasted.
2. To the pollinator or seed disperser, it would be best to be a generalist and obtain nectar and pollen from flowers or seeds in a small area, minimizing energy costs.

This casts doubt on whether there is true mutualism or whether both are trying to win an arms race. There is a way in which the plant can ensure the pollinator's/seed disperser's fidelity. That is, plants can have sequential flowering among species within years and simultaneous flowering within a species. How is it generally done? Here are some examples.

7.4.1 Senita and yucca systems

There are a large number of similarities in the independently derived mutualisms in the senita cactus–senita moth and yucca–yucca moth systems, suggesting that they have evolved in response to similar selection pressures, including selection for reduced nectar production in the plants and specialized pollen-collecting structures and active pollination behaviour in the moths. Both systems feature pollinators whose life cycles are intimately associated with long-lived plants with seasonal flowering cycles. Fleming and Holland (1998) propose that three of their common features, namely, nocturnal flower opening, self-incompatibility, and resource-limited fruit set, have been important during the evolution of obligate mutualisms. Nocturnal flower opening is important for these mutualisms because it limits the number of potential flower visitors to moths only (Thompson and Pellmyr 1992) and excludes other co-pollinators. Self-incompatibility selects for pollinators that visit flowers on different plants and, thus, both yucca moths and senita moths are under strong natural selection to be effective outcrossers. Resource-limited fruit set and reduced nectar production characterize the yucca and senita systems. Reduced nectar production may be selected for, especially when unfertilized ovules rather than nectar or pollen are the primary reward attracting pollinators, which favours the evolution of specialized pollination. Pollen limitation does not appear to be important for fruit set in either the yucca or the senita cactus. Pellmyr et al. (1996) have suggested that differences among flower visitors in pollination quality (the genetic contribution to fruit set) can favour the evolution of obligate mutualisms through selective abortion of fruits of low genetic quality.

7.4.2 Why Negev flowers are often red

There are about 15 species of large, bowl-shaped flowers of six genera from three families in the Mediterranean region of Israel (Heinrich 1994). It is dominated by buttercups of two genera. Most species in this group have a variety of colours in other parts of the world. One of these genera, *Ranunculus* has about 400 species worldwide, most of which are white or yellow (Heinrich 1994). Only 3, all in the Mediterranean, are red. All of these species have cup-shaped flowers that are far broader than those in other countries. Wild tulips (*Tulipa* spp.) are mostly yellow, yet in Israel they are red. The species in this convergent guild do not flower simultaneously. Anemones usually flower first, followed by tulips, buttercups, and poppies (Heinrich 1994). These flowers are seldom pollinated by bees. Rather, they are mostly pollinated by scarab beetles (Family Scarabeidae) of the genus *Amphiocoma*. Dafni et al. (1990) distributed unscented, flower-shaped plastic cups of various colours in the field to act as beetle traps. Of the beetles trapped in the variously coloured flower models, 127 of 148 were caught in red flower models. *Amphiocoma* do most of the pollination of the red flowers, although the red colour also advertises sex. Once they detected a red flower, they stayed to mate. The antennae are microscopic in size. Their scent organs seem almost atrophied (Heinrich 1994), but their eyes are not. Their attraction to red flowers finds mates for them (Heinrich 1994). Dafni et al. (1990) showed that these *Amphiocoma* beetles could see the colour red. This resulted in enhanced mating for them. It is not known how the red flower guild evolved, but a probable scenario is that the plants imitated one another, and that many species used the same red signal in their advertising campaigns that served to attract pollinators (Heinrich 1994). The pollinators in turn apparently preferred red over other colours (Heinrich 1994).

7.4.3 Dorcas gazelle–lily system

There are at least two cases where coevolution can be claimed in a mammal system. Owing to the almost complete removal of all flowers of the lilies by dorcas gazelles (Fig. 7.18) (there is no vegetative reproduction in this species) mentioned earlier, the lily populations in the dunes can only be maintained by seed dispersal from source populations outside the dunes where gazelles are rare or absent (owing to low lily densities in the compact loess substrate).

There is strong selection on lilies to minimize the effects of gazelle herbivory: lilies that have their bulbs partially consumed in one year are less likely to produce flowers and produce fewer, smaller leaves in the following season. Ward and Saltz (1994) found that the gazelles select lilies according to their size in a manner consistent with an optimal foraging model (Fig. 7.19).

Fig. 7.18 Dorcas gazelle (*Gazella dorcas*).

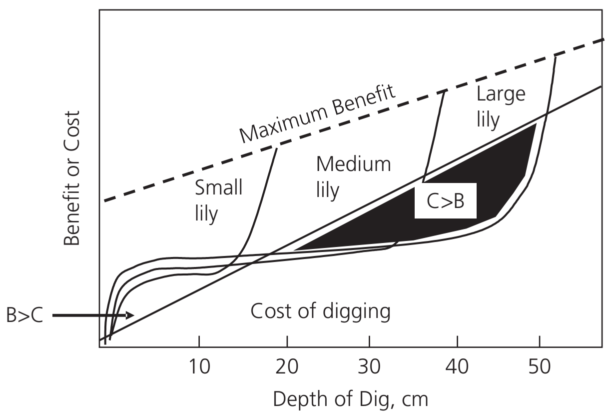

Fig. 7.19 Gazelle optimal foraging model. Gazelles should prefer small lilies because benefits exceed costs (B > C).

Source: From Ward and Saltz (1994). With kind permission of the Ecological Society of America.

As predicted by this model, contrary to popular expectation that gazelles should prefer the largest plants, gazelles should prefer the smallest plants, and not completely consume large plants. This is indeed what they do because the cost of sand removal is high (Fig. 7.19). Furthermore, when searching for leaves (leaves are available on the surface for a few months only and gazelles do not bother to dig when there are leaves), gazelles do not follow a Markov model (which assumes that there is no effect of previous search history on the gazelles) in searching for plants, and instead, focus on high densities of lilies and eat the largest lily leaves once there.

Lilies also grow in ways that are consistent with coevolution. These lilies grow their bulbs down deeper into the sand (pulling them down with contractile roots) to minimize the effects of herbivory in populations where gazelles are common but have bulbs under the surface in populations where gazelles are absent (Ward et al. 1997, 2000a). Lilies protect their leaves with calcium oxalate crystals (called 'raphides')—gazelles eat only the unprotected tips (Figs. 7.20a and b).

Lily populations where gazelles are common have more crystals in their leaves than where gazelles are absent (Ward et al. 1997; Ruiz et al. 2002). Ruiz et al. (2002) considered this to be a form of constitutive defence (i.e. unlike inducible defences, the strategy does not change when there is herbivory), because adding more calcium to the sand did not increase investment in defence (Fig. 7.21).

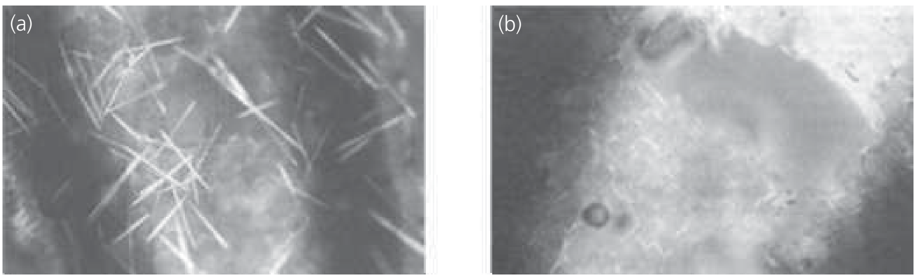

Fig. 7.20 Raphide photos, (a) with and (b) without raphides of calcium oxalate (from 1 cm near tip of leaf).

Source: From Ward et al. (1997). With kind permission of Springer.

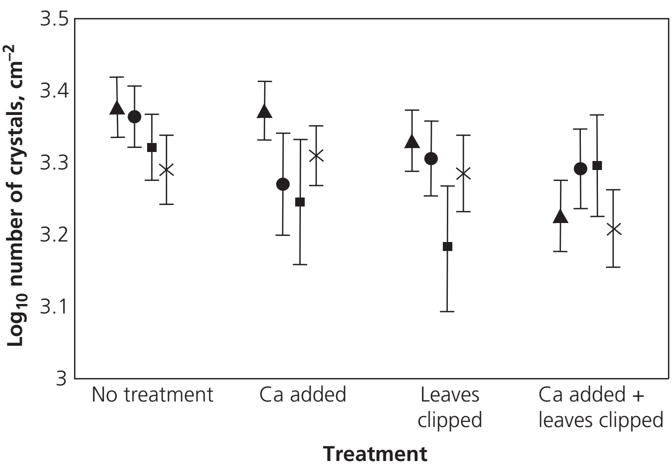

Fig. 7.21 Ruiz et al. (2001) showed that raphides were a constitutive defence because there was no effect of calcium supplementation or herbivory.

Source: From Ruiz et al. (2001). With kind permission of Blackwell.

This study demonstrated that calcium oxalate is produced in leaves to protect them against herbivory—raphides in geophytes had previously been assumed to have developed as a consequence of excessive calcium uptake from the soil (Franchesci and Horner 1980). The close coevolution of the gazelle (optimal foraging behaviour in terms of both size of plant consumed and search behaviour, and avoidance of chemically defended parts of leaves) and the lily (evolution of deeper bulbs and chemical investment in leaves) indicates that strong biotic interactions between herbivore and plant can and do develop in arid regions in spite of the great impact of abiotic factors on plant populations.

7.4.4 Wood rats and their toxic diets

Desert woodrats, *Neotoma lepida*, are renowned for their abilities to forage on toxic plants (Mangione et al. 2000). Mangione et al. (2000) studied the tolerance of these woodrats to phenolic resin from the creosote bush, *Larrea tridentata*, in two populations of *Neotoma lepida*. One of these populations, in the Mojave Desert, encounters and eats creosote bush (= experienced population), while the other population from the Great Basin Desert has no creosote bushes (this population mostly eats juniper, *Juniperus osteosperma*) and consequently is a naïve forager on creosote bushes. Experienced woodrats from the Mojave population maintained body mass for longer on increasing amounts of phenolic resin than the naïve counterparts from the Great Basin Desert. Subsequently, Kohl et al. (2014) showed that gut microbes were crucial in allowing desert woodrats to consume *Larrea tridentata*. They also found that treatment with antibiotics disrupted the ability of woodrats to consume creosote bush toxins. They also did microbial transplants into naïve woodrats from experienced donor woodrats and found that microbes could enhance the ability of naïve woodrats to consume creosote resins. This is not merely a demonstration of phenotypic plasticity; Kohl et al. (2014) consider there to be some measure of host adaptation because woodrats from 'experienced' populations were able to consume more creosote resin than the naïve individuals. Magnanou et al. (2009) believe that this is due to unique adaptations of their hepatic detoxification machinery. Kohl et al. (2014) believe that there are three ways that woodrats may acquire novel detoxifying microbes in nature: (1) Microbes may come directly from plants (Kohl et al. 2014). (2) Herbivores engage in geophagia (soil consumption) to adsorb toxins (Vorhies and Taylor 1940; Krishnamani and Mahaney 2000). (3) Woodrats frequently collect and store faeces from jackrabbits, coyotes, and cows (Betancourt et al. 1990).

Torregrossa et al. (2012) studied two other species of desert-dwelling woodrat, *Neotoma stephensi* (a specialist on junipers) and *Neotoma albigula* (a generalist herbivore) (Fig. 7.22). Specialist herbivores could reasonably be expected to have evolved biotransformation pathways that can process large doses of secondary compounds from the plant species on which they specialize (in this case, the juniper). This may result in a trade-off, limiting the ability of specialists to ingest novel plant secondary metabolites (PSMs) such as are contained in the creosote bush (see earlier). In contrast, the generalist foraging strategy requires that herbivores alternate consumption

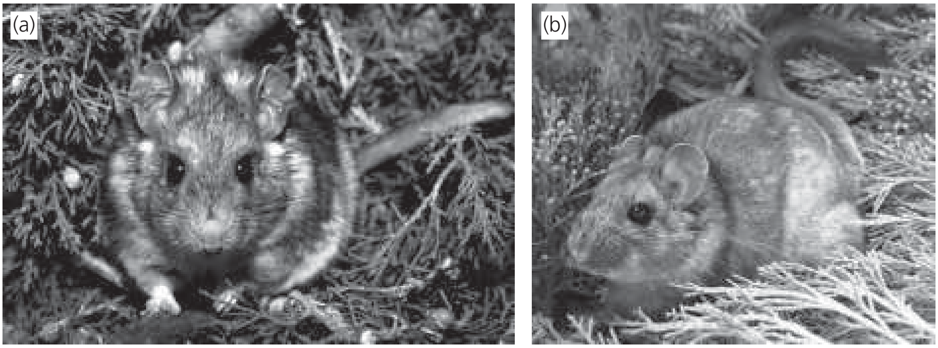

Fig. 7.22 Desert-dwelling woodrat, (a) *Neotoma stephensi* (a specialist on junipers) and (b) *Neotoma albigula* (a generalist herbivore).

Source: Photos courtesy of M. Denise Dearing (a) and Kevin Kohl (b).

of plant species (Westoby 1974) and/or types of PSM to reduce the possibility of over-ingestion of any particular PSM. The ability to behaviourally regulate is a key component of this strategy. Torregrossa et al. (2012) found that the specialist (*Neotoma stephensi*) lost more mass than the generalist (*Neotoma albigula*) during the experiment. In addition, although both species regulated phenolic resin intake by reducing meal size while on the highest resin concentration (4%), the generalist (*Neotoma albigula*) began to regulate intake on the 2% diet. The ability of the generalist to regulate intake at a lower PSM concentration may be the source of the generalist's (*Neotoma albigula*) performance advantage over the specialist (*Neotoma stephensi*). Thus, there is evidence from three species, one (*Neotoma lepida*) with two populations with different evolutionary histories and a comparison of two species (*Neotoma stephensi, Neotoma albigula*) with different dietary strategies, that there is coevolution of mammals and their physiological and behavioural abilities to consume novel PSMs.

8 Desert Food Webs and Ecosystem Ecology

Ecosystem ecology has developed from a number of fields and attempts to link, among other issues, trophic dynamics (feeding relationships among organisms), food webs (e.g. Fig. 8.1), and biogeochemistry (biological influences on chemical processes in ecosystems) (Hagen 1992; Chapin et al. 2011). One of the most important contributions to ecosystem ecology was made by Jenny (1941). Jenny (1941) considered ecosystem functioning to be controlled by five independent control factors. These state factors are climate, parental materials (rocks that create soils), topography, potential biota (organisms occurring in the environment that could potentially invade that ecosystem), and time (Chapin et al. 2011). Clearly, parent materials and topography are not truly independent in the sense that some parent materials erode more quickly than others so that, for example, one might frequently find that softer sandstone habitats have an inclined topography while granite and basalt are harder substrates and erode only at their peripheries, leaving an abrupt disjunction between these and softer substrates. Jenny's (1941) state factor approach was a major conceptual advance in ecosystem ecology because it changed ecosystem ecology from a simple description of patterns to one that emphasized the controls over processes. Furthermore, it also indicated an experimental approach to test the importance and mode of action of each control. Here, I will emphasize trophic dynamics and describe some desert food webs and then I will consider some important ecosystem approaches that are necessary for a better understanding of how the desert environment works.

8.1 Do deserts have simple food webs?

Deserts have simple food webs if the animals involved are small. For example, if the animal eating plants is relatively large (e.g. a dorcas gazelle (*Gazella dorcas*), which weighs about 15–20 kg), it can only really be preyed upon by leopards (*Panthera pardus*) and perhaps striped hyaenas (*Hyaena hyaena*) in the Negev Desert (Israel). In such a case there are only three links in the trophic chain or pyramid [plants–gazelles–leopards]. In the Namib Desert, Holm and Scholtz (1980) record that the herbivorous coccid hemipteran (*Aclerda* sp.) may be eaten

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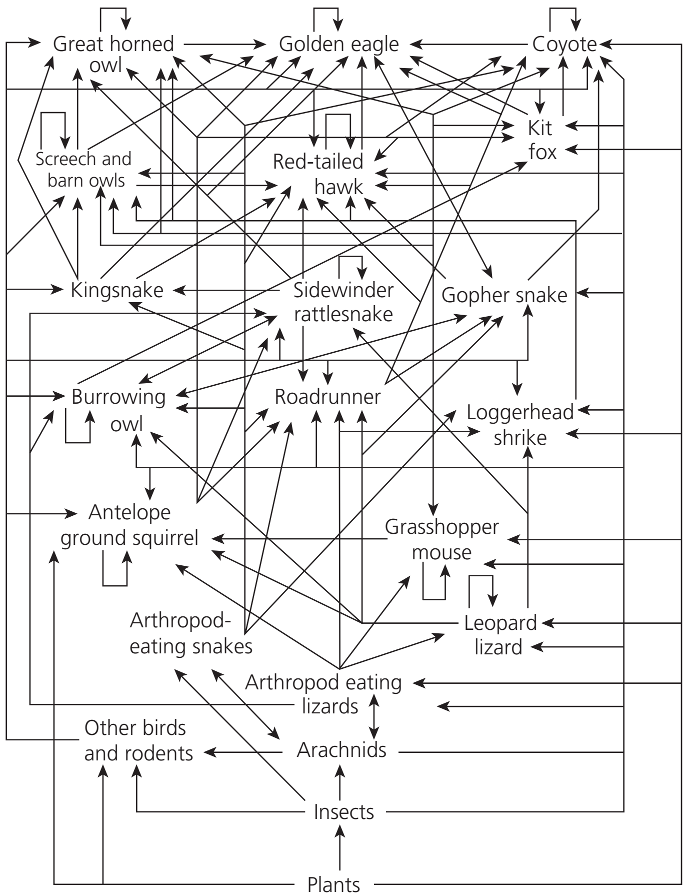

Fig. 8.1 Food-web interactions involving a few of the 96 vertebrates resident in the arid Coachella Valley. Note that the bottom of this web is simplified from other webs.

Source: From Polis (1991). Kind permission of University of Chicago Press.

by the Namib golden mole (*Eremitalpa granti namibensis*), which is eaten by black-backed jackals (*Canis mesomelas*) and/or brown hyaenas (*Hyena brunnea*), with just four links in the trophic pyramid. Alternatively, *Aclerda* sp. may be eaten by spiders, solpugids, and/or scorpions, which are eaten by the lizard (*Aporosaura anchietae*), which is eaten by snakes such as Peringuey's adder (*Bitis peringueyi*), which are subsequently eaten by raptorial birds such as the greater kestrel (*Falco rupicoloides*) or pale chanting goshawk (*Melierax canorus*) or even the spotted eagle owl (*Bubo africanus*), resulting in six links in the trophic pyramid (Holm and Scholtz 1980). In the Negev Desert, if the main consumers are macrodetritivores and are small (e.g. tenebrionid beetles), then they can be preyed upon by slightly bigger organisms (let us say a *Latrodectus revivensis* spider), which in turn can be preyed upon by a great grey shrike (*Lanius *excubitor*), which can be preyed upon by a rock kestrel (*Falco tinnunculus*). In this second case, there are also six links in the trophic chain [plants–detritus–termites–spiders–shrikes–kestrels]. Ayal et al. (2005) found that if the animals at the bottom of the chain are small, then more steps can be incorporated as one moves up the chain.

8.1.1 Can we scale up from two-species interactions to desert ecosystems?

We cannot scale up from two-species interactions. Ecological complexity can emerge from the existence of environmental heterogeneity and scaling effects (Proulx 2007). The effects of scaling include the different changes in patterns produced by processes that occur at different temporal and spatial scales (Ziv et al. 2005; Wheatley and Johnson 2009; Thibault et al. 2010b). For example, the interspecific competition that has been recorded in various studies in the Negev Desert with rodent species (Wasserberg et al. 2007; Scharf et al. 2008; Kotler et al. 2010) and in the Chihuahuan Desert (Ernest et al. 2008) may strongly influence species coexistence at the local (α) diversity scale but may be unimportant at the regional (γ) diversity scale because colonization and extinction dynamics may be more important than local diversity (Ziv et al. 2005). A similar situation may exist for plants that benefit from one another (facilitation) and later compete with each other (Dean et al. 1992; Munzbergova and Ward 2002; Miriti 2006; Seifan et al. 2010; Butterfield and Briggs 2011).

Environmental heterogeneity may result from habitat diversity (the number of different habitats), habitat size, and habitat patchiness (the continuity of a patch in a landscape) (Ziv et al. 2005). Each of these components may influence species diversity and degree of interaction by the ways in which they are affected by coexistence, colonization, and extinction effects (Brose 2010). As indicated by Proulx (2007) and Wheatley and Johnson (2009), different spatial and temporal scales may influence the ways that organisms respond to their environments. This has led scientists to concur that scale itself (whether spatial or temporal) is an important subject for study (Wiens et al. 1993; Wheatley and Johnson 2009).

For the reasons outlined earlier, I focus on trophic levels and, more closely, on food webs. Many ecologists have considered trophic levels to be somewhat redundant (see Cousins 1987 and references therein) and urge that we focus on food webs because of the far greater realism involved in them. Nonetheless, some (Ayal et al. 2005) have argued that trophic levels help to simplify our understanding of the interactions between parts of the ecological pyramid and have also indicated that even food webs have their problems because a food web quickly degenerates into a series of lines and arrows with little indication, if any, of the relative importance of some interactions. However, food-web theorists have recognized that presence–absence relationships are not nearly as convincing as quantitative relationships between the relative abundances of organisms at different trophic levels (Williams and Martinez 2000; Ings et al. 2009).

8.2 Food webs

In the most well-known desert food web studied to date, Polis (1991) studied the Coachella Valley web (Mojave Desert, North America) and found that predators eat from all trophic levels. Polis (1991) found that consumers may eat all trophic levels of arthropods in addition to plant material and vertebrates (Fig. 8.1). This creates a problem of assigning a specific trophic level to a species that varies ontogenetically, seasonally, or even opportunistically. Polis (1991) also found the following:

1. Longer chain lengths may occur in deserts than elsewhere (6–11 links are common, in comparison with average lengths of 2.7–2.9 published elsewhere). Indeed, Schoener (1989) showed that some deserts may have the most links in their chains of any habitat, regardless of whether it was terrestrial or freshwater (Table 8.1; data from Briand and Cohen 1987). This probably depends on the size of the organisms at the bottom of the chain, with small organisms facilitating more complex chains (Holm and Scholtz 1980; Ayal et al. 2005). An interesting similarity to Polis' Coachella Valley web is found in Holm and Scholtz's (1980) food web from the Namib Desert dunes (Fig. 8.2). The Namib Desert web also contains many links in the chain.

Table 8.1 Maximum web length in terrestrial habitats

Maximum number of trophic links	Web
2	Salt meadow—New Zealand
3	Willow communities—aspen parkland, U.S.A.
3	Barren regions—Spitsbergen
3	Reindeer pasture—Spitsbergen
3	Rain forest—Malaysia
3	High Himalayas—India
3	Tundra—Prudhoe, Alaska, U.S.A.
4	Salt marsh—terrestrial portion
4	Prairie—aspen parkland, U.S.A.
4	Wytham wood—Oxford, U.K.
4	Trelease woods—Illinois, U.S.A.
4	Wet tundra—Barrow, Alaska, U.S.A.
4	Rajasthan Desert—India
5	Kaibab plateau—forest and adjacent grassland
5	Coniferous forest—Japan
6	Namib Desert dunes—Namibia

Source: Modified from Schoener (1989); data from Briand and Cohen (1987).

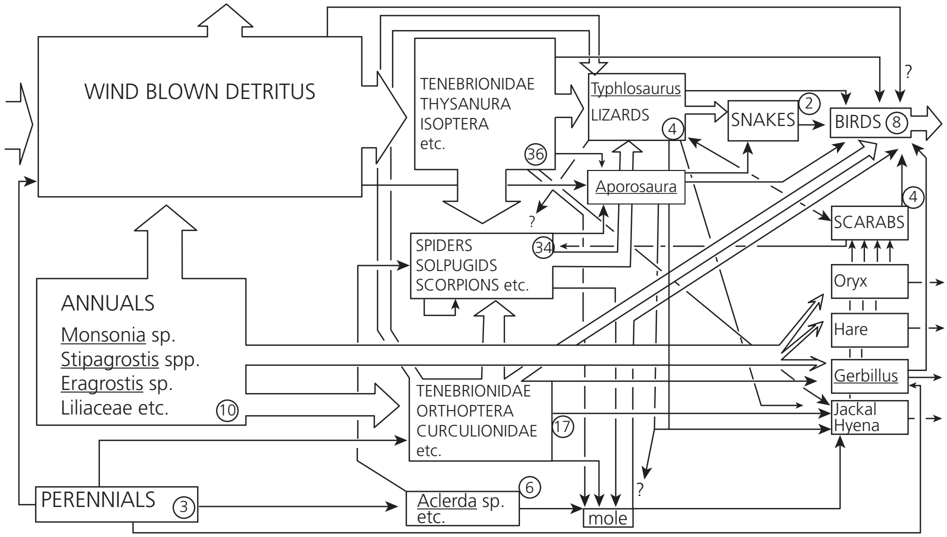

Fig. 8.2 Food web of the dune ecosystem near Gobabeb, Namib Desert, Namibia. Circled numbers are numbers of species in the various trophic categories. Widths of arrows reflect crude estimates of energy flow.

Source: From Holm and Scholtz (1980).

2. Omnivory and looping are not rare. Looping (one species eats another and vice versa) can be especially true of cannibalism. Also, ontogenetic reversal of predation can occur. For example, desert gopher snakes (*Pituophis catenifer deserticola*) eat eggs and young of burrowing owls (*Athene cunicularia*), while adult burrowing owls eat young gopher snakes (Polis and Yamashita 1991). Normal mutual predation can also be important, for example, ants involved in territorial battles eat each other.
3. There is an absence of compartmentalization. An early review by Pimm and Lawton (1980) also found little evidence of compartmentalization. Pimm and Lawton (1980) considered compartments to consist of links that formed subsystems that had little linkage with other trophic units. They considered most such compartments to constitute different habitats. However, this has been reconsidered (Allesina and Pascual 2009; Guimera et al. 2010) and can include highly interacting nodes such as diurnal versus nocturnal and aboveground versus belowground (Wardle et al. 2004). Extensive crossover in the arid Coachella Valley exists. Foraging times change from day to night as a function of temperature; for example, nocturnal species eat diurnal prey (e.g. scorpions eat robberflies). Plants and detritus are eaten during all periods by species that live above and below the surface. Arthropods feeding below ground export energy when they become surface-dwelling adults (e.g. beetles) (Polis 1991).

8.2.1 Polis and Ayal's problems with food-web models

Polis (1991, 1994, 1997) and Ayal et al. (2005) note that the assumptions of food-web models, such as the 'cascade' model of Cohen (1989), are not correct for many invertebrate-dominated webs. Polis (1991) found that actual food webs are much more complex than those described by previous workers. Polis (1991) found the following:

1. Energetics is not necessarily the most appropriate way to view food webs. This point has been conceded by food-web theorists (e.g. Schmitz et al. 2004; Allesina et al. 2008; Kefi et al. 2012).
2. Interaction webs (describing population effects) and descriptive webs (quantifying energy and matter flow) are not necessarily congruent (see also Kefi et al. 2012).
3. Another way of saying the previous point is that an apparently weak link (in terms of diet or energy transfer) can be a key link dynamically (e.g. parasites can regulate predator populations but accumulate little energy, following Oksanen et al. 1981; Oksanen and Oksanen (2000); see Fig. 8.3).
4. Consumer regulation of populations need involve little energy transfer and few feeding interactions.
5. Polis (1991) had a problem with the lumping of species according to body size contra 'trophic species' of Cohen (1989), who lumped species of similar body size and trophic habit into a single species. Raffaelli (2007) essentially defends Cohen (1989) because he considers that when predators or herbivores eat their prey, the main issue that they need to take into account is whether the prey is small enough to ingest or stands still long enough to be eaten without incurring damage through toxins or physical attack. Thus, body size is of primary importance. The issue of allometric scaling of body size to food-web interactions has subsequently been supported by a number of authors (e.g. Memmott et al. 2000; Woodward

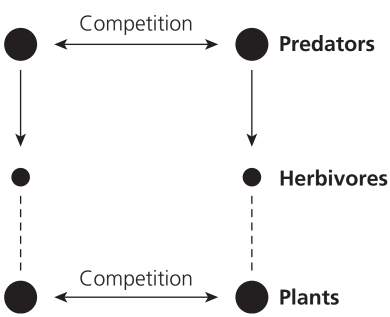

Fig. 8.3 An apparently weak link (in terms of diet or energy transfer) can be a key link dynamically (e.g. parasites can regulate predator populations but accumulate little energy). Sizes of circles indicate magnitudes of effects rather than population sizes.

Source: Modified from Oksanen et al. (1981). With kind permission of University of Chicago Press.

et al. 2005; Petchey et al. 2008; Williams et al. 2010). I note that Verdu et al. (2010), Eklöf et al. (2012), and Naisbit et al. (2012) found that phylogeny was as important a factor as body size. In particular, Naisbit et al. (2012) found that phylogeny was a more important factor than body size, although they too recognize that body size is an important component of food-web interactions.

8.3 Interactions among habitats—spatial subsidies

Spatial subsidies between webs can make food-web theories more complicated (Knight et al. 2005; Leroux and Loreau 2008). Often, consumers in one system are subsidized via consumption from another web in a different habitat (Leroux and Loreau 2008). This is called a donor-controlled interaction because the consumers have no effect on the other web. Their populations are maintained at high levels, which may allow top-down effects in their 'home' web not possible solely with *in situ* productivity. As an example of a spatial subsidy, Polis and Hurd (1996) found in the Namib Desert coastal system that black widow spiders (*Latrodectus indistinctus*, Theridiidae) suppress herbivores on dune plants, but high spider populations are actually maintained by feeding on detrital-algae-feeding flies from the marine system next door.

In North America, marine input supports abundant detritivore and scavenger populations on desert coasts (Polis et al. 1997). Some of these consumers fall prey to local and mobile terrestrial predators. In the Baja California desert system of North America, insects, spiders, scorpions, lizards, rodents, and coyotes are 3–24 times more abundant on the coast and small islands than on inland areas and large islands (Polis and Hurd 1996; Rose and Polis 1997). In Baja, coastal spiders are six times more abundant than inland spiders. Their diets, as confirmed by ^{13}C and ^{15}N stable isotope analyses, are significantly more marine-based than are those of their inland counterparts (Anderson and Polis 1998). In addition, on the Baja mainland, coastal coyotes eat ~50% mammals and ~50% marine prey and carcasses (Rose and Polis 1997). There, coastal rodent populations are significantly less dense than on islands lacking coyotes, suggesting that marine-subsidized coyotes depress local rodent populations. In the hyper-arid Peruvian section of the Atacama Desert (mean annual rainfall = 2 mm), Catenazzi and Donnelly (2007) found that, despite the absence of an effect of El Niño currents (unlike the Baja California example where there is a strong effect of El Niño), the marine green alga *Ulva* had a strong effect via the invertebrates that forage on it. Large effects higher up the food chain were seen on geckos (*Phyllodactylus angustidigitus*, Gekkonidae), solifuges (*Chinchippus peruvianus*, Ammotrechidae), and scorpions (*Brachistosternus ehrenbergii*, Bothriuridae).

Delibes et al. (2015) used stable isotopes to study niche use in ten populations of orange-throated whiptail lizards (*Aspidoscelis hyperythra*), which consumes arthropods in ten localities of Baja California Sur (Mexico). These localities ranged from arid to subtropical. They found that localities close to sea level were more likely to be enriched in ^{15}N, indicating marine subsidies although they recognized this was mostly at an individual level. They also found that lizards from more arid habitats were more enriched in ^{13}C, indicating that the origin of their arthropod foods came from the consumption of succulent CAM plants and to a lesser extent from C_4 grasses. Contrastingly, lizards from subtropical sites had more C_3 plants in their diets, indicating that the origins of their foods came from shrubs and trees.

Worldwide, nutrient budgets of many terrestrial ecosystems depend on aerial transfer of nutrients. For example, in much of the Amazon Basin, soils are nutrient-poor due to limited river deposition and extreme leaching (Swap et al. 1992). Phosphorus, which is an element that limits net primary productivity (after nitrogen, according to Liebig's law), may be transferred intercontinentally. About 13–190 kg ha^{-1} $year^{-1}$ is carried by dust blown from the Sahara 5,000 km away (Swap et al. 1992). Such input doubles the standing stock of phosphorus over 4,700–22,000 years. Thus, the productivity of Amazon rainforests depends on fertilization from another large ecosystem, the Sahara. Clearly, these two ecosystems are separated by an ocean, yet they are still atmospherically coupled (Swap et al. 1992). Another example of long-distance transfer of dust occurs off the coast of Namibia (Fig. 8.4). Dust plumes can seriously affect marine ecosystems, not least by altering the amount of iron in circulation. This

Fig. 8.4 Dust plumes off the coast of the Namib Desert, Namibia.
Source: Photo courtesy of N.A.S.A.

affects the ability of some marine phytoplankton known as diazotrophs to fix nitrogen from nitrogen gas in the atmosphere into a more useful form, such as ammonia (Sohm et al. 2011) by reducing or eliminating iron limitation to diazotrophs. In some cases, where there are coral reefs, desert dust may even reduce zooxanthellae symbioses (Garrison et al. 2003) and even cause death of corals by transporting toxic micro-organisms to the corals (Rypien 2008).

8.4 Effects of precipitation, nutrients, disturbances, and decomposition

I consider here the effects of precipitation (which can come as rainfall, fog, or snow) and nutrients as well as disturbances (which can be as important as nutrient changes) on ecosystem ecology, and also relate this to decomposition processes.

8.4.1 Effects of precipitation

Noy-Meir (1973) listed three attributes of arid ecosystems:

1. Total precipitation is so low as to ensure that water is the dominant factor for biological processes.
2. Precipitation is highly variable throughout the year (and spatially) and occurs in infrequent and discrete events.
3. Variation in precipitation is unpredictable.

This led to the creation of the pulse-reserve paradigm (see Noy-Meir 1973), where a rain event triggers a *pulse* of activity. Some of the rain is lost either to consumption and/or mortality and the remainder is committed to a *reserve* such as seeds or storage (as in geophytes or succulents). The magnitude of the pulse depends on the season (e.g. rainfall in mid-summer in the Arabian Desert will have little or no effect on growth and survival because rainfall mostly comes in spring) and size and duration of the precipitation event. In general, therefore, deserts are pulse-driven ecosystems; that is, precipitation occurs erratically in pulses rather than continuously (Schwinning et al. 2004). It is also noteworthy that nitrogen may place a limit on productivity (Austin 2011), at least during periods of adequate moisture. Reynolds et al. (2004) have developed a modified model of the pulse-reserve system that they believe is more general in that it takes antecedent conditions in the soil (e.g. how much rain has previously fallen and how recently it fell and soil type) and plant functional type into consideration (Fig. 8.5). Reynolds et al. (2004) consider that productivity is not a response to individual-pulsed events per se but rather to soil water recharge and availability, which can be affected by soil type, topography, atmospheric conditions as well as current plant cover and biomass, all of which can interact in a multitude of non-linear ways. Nonetheless, Reynolds et al. (2004) still support the pulse-reserve model but are a little contentious of its details.

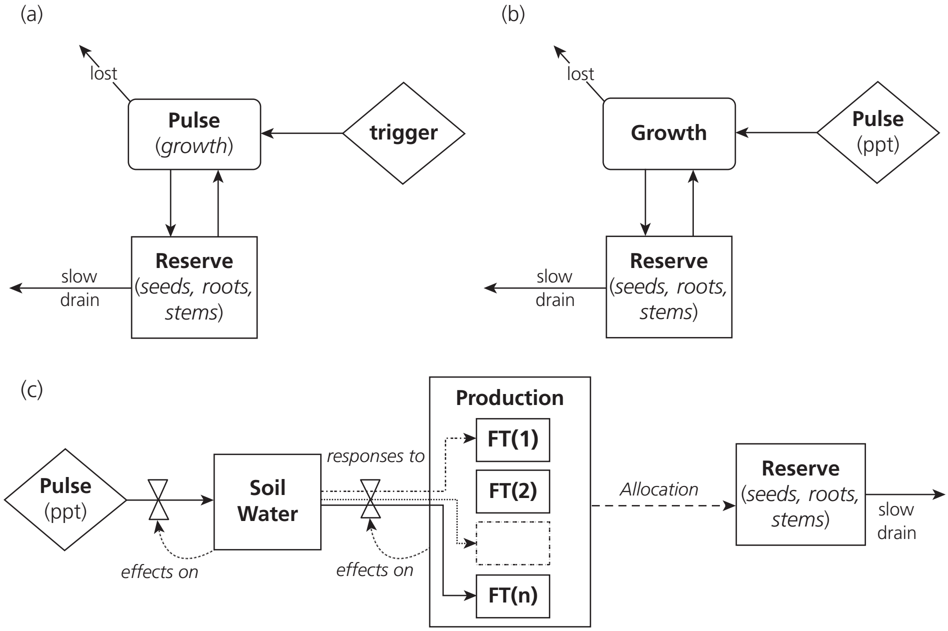

Fig. 8.5 Three types of pulse-reserve models. (a) Pulse-reserve model of Bridges and Westoby (unpubl. data, presented in Noy-Meir 1973). (b) Common interpretation of pulse-reserve model in which 'pulse' events are equated with the triggering events of precipitation, rather than with a pulse of growth as envisioned in (a). (c) Reynolds et al. (2004) have developed a modified model of the pulse-reserve system that they believe is more general in that it takes antecedent conditions in the soil (e.g. how much rain has previously fallen, how recently it fell, as well as soil type) and plant functional type into consideration. FT = plant functional type.

Source: From Reynolds et al. (2004). With kind permission of Springer.

Rainfall pulses mostly are less than 2 mm and few exceed 10 mm (Fig. 8.6). Biological soil crusts probably play the major role in carbon fluxes in hot deserts because most rainfall events are less than 2 mm (Belnap et al. 2001; Cable and Huxman 2004). However, there are many other studies that have shown that responses to precipitation increase with the amount of precipitation (e.g. Le Houérou 1984; Gutierrez and Whitford 1987; Gutierrez et al. 1988; Stephens and Whitford 1993).

Sher et al. (2004) have also shown that interpulse interval (i.e. number of days between rain events) had important effects on the survival of annual plants in the Negev Desert (Israel). They found that reduced interpulse intervals had a positive effect on survival (Fig. 8.7) and, in some cases, on growth.

Noy-Meir (1973) and Beatley (1974) noted the importance of precipitation thresholds for triggering germination events and predicted that recruitment into populations for long-lived plants should be triggered by rare rainfall events of large magnitude. For example, Joubert et al. (2008) found that three successive years

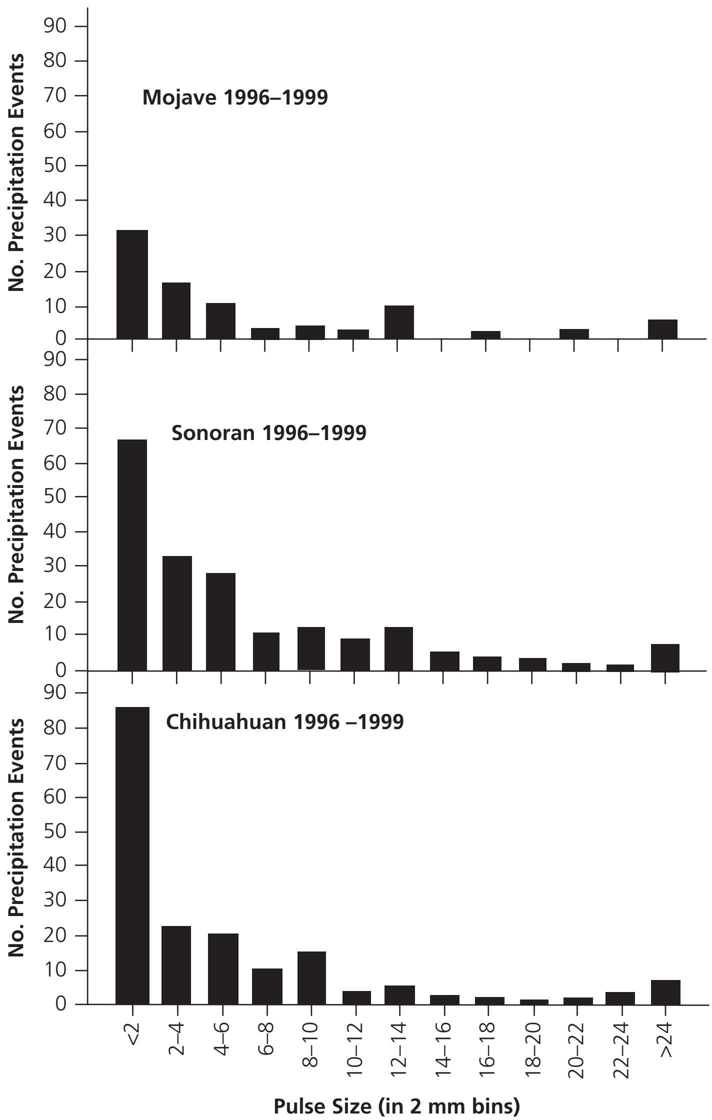

Fig. 8.6 Number of rainfall events of particular pulse sizes for the Mojave, Sonoran, and Chihuahuan deserts. Most of these pulses are less than 2 mm and few exceed 10 mm.

Source: From Cable and Huxman (2004). With kind permission of Springer.

of above-average rainfall (>500 mm MAP) were needed for establishment of *Acacia mellifera* in the ProNamib in Namibia. Wiegand et al. (2004) examined this with regard to *Acacia* trees germinating in Israeli deserts and found that large, rare events were important for germination and smaller, pulsed events could be important for population dynamics, especially because the maintenance of populations

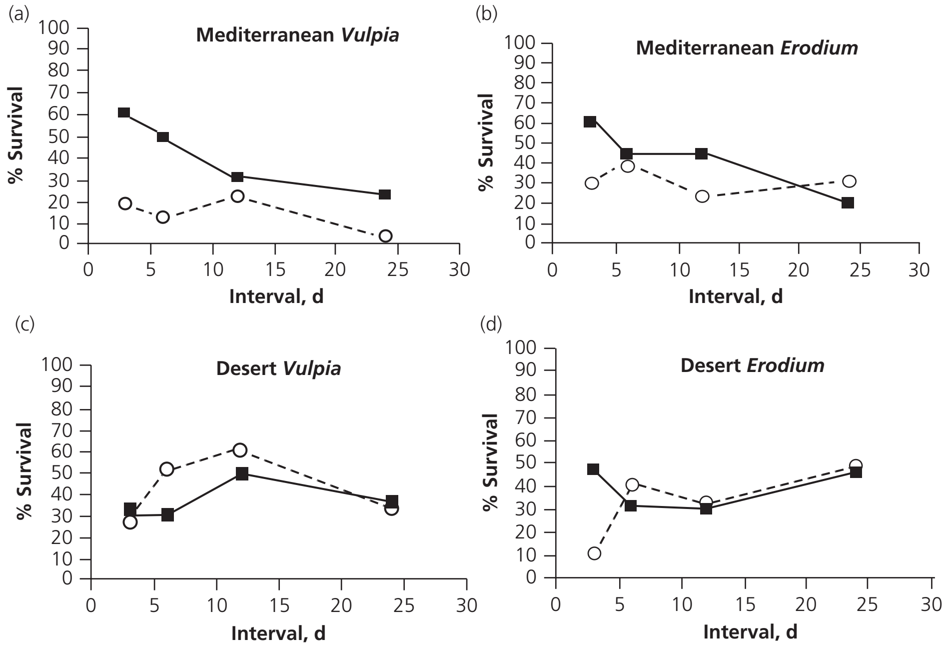

Fig. 8.7 (a–d) Sher et al. (2004) have also shown that interpulse interval (i.e. number of days between rain events) had important effects on the survival of annual plants in the Negev Desert (Israel). They found that reduced interpulse intervals had a positive effect on survival and, in some cases, on growth. Black squares = high rainfall (500 mm/season); clear circles = low rainfall (100 mm/season).

Source: From Sher et al. (2004). With kind permission of Springer.

of long-lived trees such as these requires frequent post-recruitment rainfall to allow the trees to survive through the crucial first year.

Ecological processes in deserts usually experience brief periods in which there is sufficient available water (Noy-Meir 1973; Knapp et al. 2008). Consequently, ecological processes are often described in terms of pulse dynamics (Noy-Meir 1973), with long periods of dryness followed by short periods of adequate water availability. Pulses of water act as transport vectors, erode landscapes, alter soil microenvironments, and create disturbances in addition to providing adequate water to plants. Rain also results in increases in grass fuel loads, which may lead to wildfires or even alter the probability of shrub encroachment (also known as woody plant encroachment) because grasses typically outcompete trees and shrubs (Kraaij and Ward 2006; Grellier et al. 2012; Vadigi and Ward 2014; Tjelele et al. 2015).

Collins et al. (2014) have stressed that an expanded framework needs to be developed so as to more accurately demonstrate how pulsed rainfall events affect arid ecosystems. They propose a hierarchical pulse-dynamics framework to provide a more extensive picture of the relationships between exchanges of nutrients and energy between organisms and the environment. Collins et al. (2014) also note that a pulse-dynamics framework is different from the pulse-reserve system listed earlier. They note that an example of a pulse-reserve exists in the form of accumulating net primary production through a growing season, resulting in a pulse-reserve due to carbon fixation and biomass production (Reynolds et al. 2004; Collins et al. 2008). However, the reverse can also occur. For example, processes such as soil respiration deplete reserves rather than create them (Sponseller 2007). Also, while nitrogen mineralization matches moisture availability, nitrogen uptake by plants as well as microbes results in the consumption of all available nitrogen without any reserve remaining (Carreira et al. 1994; Dijkstra et al. 2012).

The multiscaled, hierarchical pulse-dynamics framework (HPDF) described by Collins et al. (2014) integrates space and time by concentrating on the following four pulse-related processes, viz. exchanges, interactions, transitions, and transfers (Fig. 8.8). These occur over a range from individual to multiple pulse events and extend from microscale to a watershed scale.

The lowest level of the HPDF focuses almost exclusively on event-scale pulse responses that have been widely studied because this level is most directly related to the original pulse-reserve model. These event-scale responses to rainfall pulses focus largely on exchanges between soils and biological crusts (also known as biocrusts or biological soil crusts (BSC)) and between microbial communities and plants (with increases in response to wetting of the soils; Vishnevetsky and Steinberger 1997; see also Belnap 2006). Biocrusts consist of a layer of photosynthetic and heterotrophic micro-organisms concentrated at or a few millimetres below the soil surface occur on up to 70% of arid-land soils (West 1990; Pointing and Belnap 2012). Biological crusts fix both atmospheric carbon and nitrogen and are important sources of nitrogen and carbon to desert soils (Elbert et al. 2012). Biological crusts are also an important source of fixed nitrogen at a global scale (Elbert et al. 2012). Because of their substantial cover, they also represent an interface of exchange between soil and atmosphere through which most pulse-driven inputs and losses to desert soils must pass (Fig. 8.9). From this lowest level, the Collins et al. (2014) HPDF links both spatial and temporal scales by joining exchanges to population dynamics and species interactions, and then to the various ways that interactions among populations and species and population responses can lead to ecosystem transitions, such as shrub encroachment or tree mortality. The highest level of the HPDF addresses the large-scale consequences of these transitions primarily in response to high-intensity rain events (Collins et al. 2014). At larger spatial scales and over longer (decadal) time periods, transitions and ecotone shifts may occur as species interactions respond to changes in precipitation amount, intermittency, and seasonality (Fig. 8.8). These transitions are often abrupt and irreversible, suggesting that the observed transitions represent a shift between alternative stable states (Noy-Meir 1975; Beisner et al. 2003; D'Odorico et al. 2012). Some ecosystem states have low resilience to changes in environmental conditions or disturbances, driving them across a critical threshold into a 'new' alternative state (Beisner et al. 2003). The system may then remain locked in this new state even after the external drivers (e.g. drought, disturbances) return to

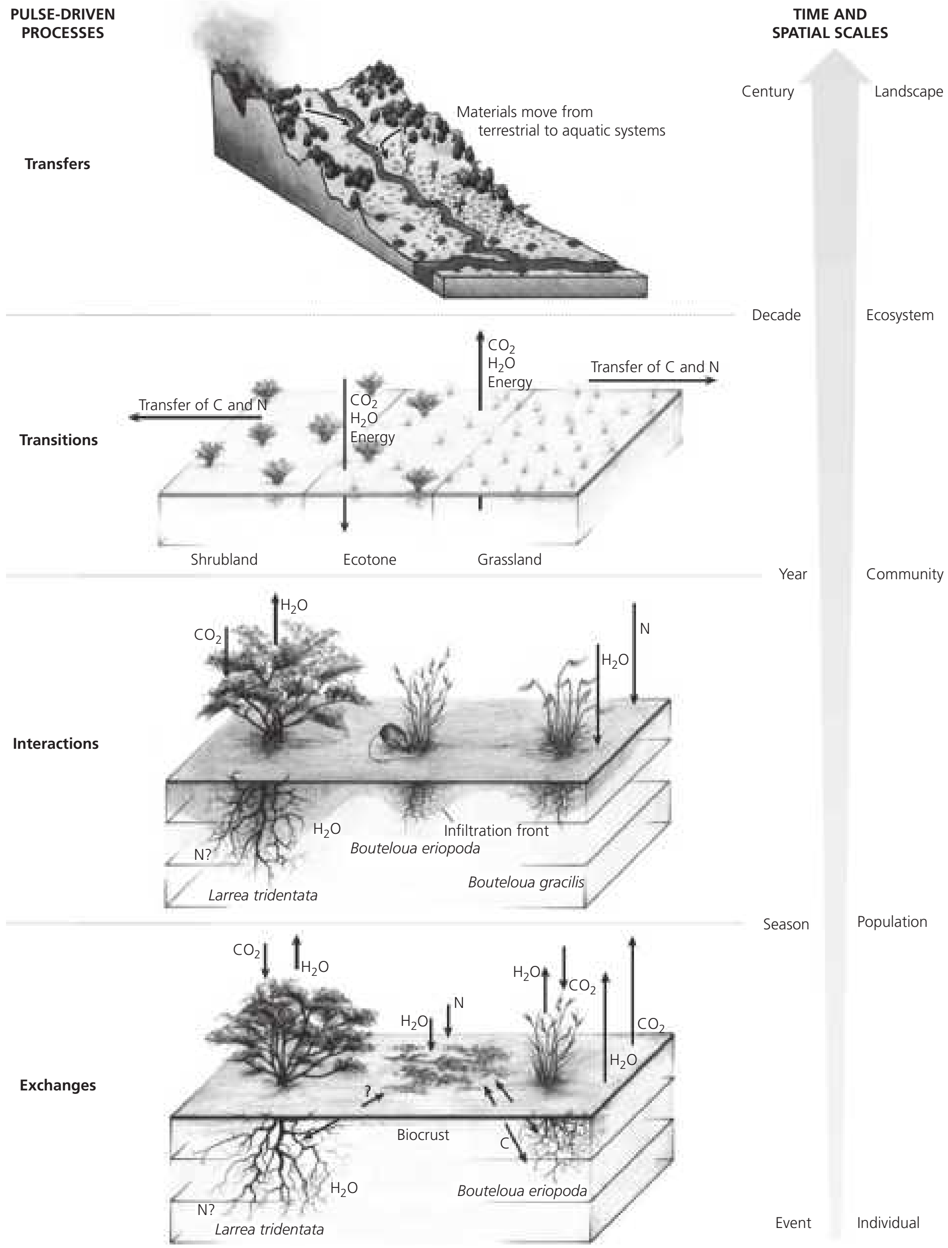

Fig. 8.8 Components of the hierarchical pulse-dynamics framework focus on exchanges of nutrients and energy between organisms and the environment that occur in response to single or multiple water pulses within a growing season; interactions between species, within and among years; transitions within a landscape over years to decades; and rain-event-mediated transfers of materials among landscape units.

Source: Images drawn by Natalia Roberts. From Collins et al. (2014). With kind permission of Annual Reviews.

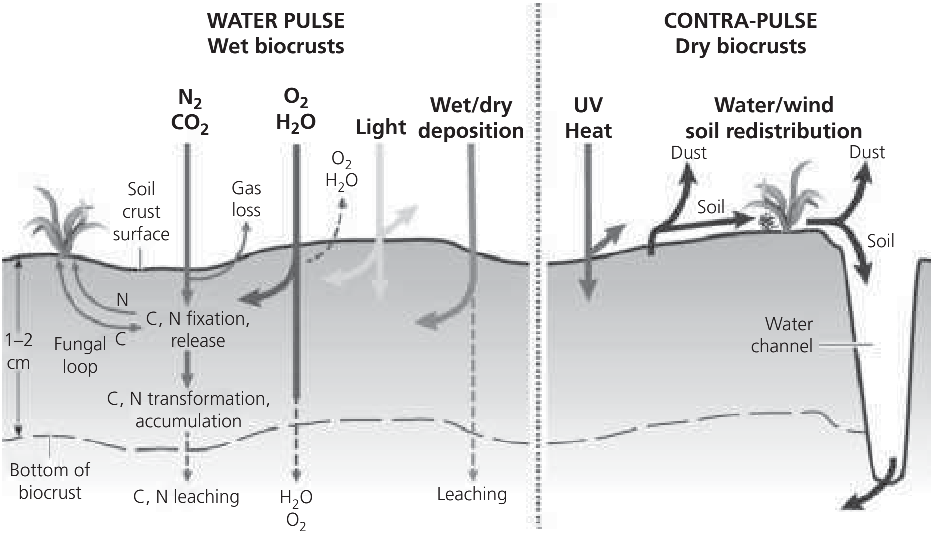

Fig. 8.9 Diagram of the various types of materials and energy crossing the atmosphere–biological crust boundary. The left side of the diagram depicts processes that occur after a water pulse; the right side presents contra-pulse processes that occur when biological crusts and underlying soils are dry. In effect, the soil–atmosphere boundary is conceptually analogous to a cell membrane. Smaller molecules (water, carbon dioxide) diffuse through the biological crust boundary, whereas larger, more complex molecules, or materials (e.g. complex carbohydrates) move via 'active transport' by the vascular plants that extend above and below the soil surface and water as it carries materials (e.g. organic matter, dust, nutrients, seeds) into the soil. The size of the arrows indicates the relative amount of material/energy entering or leaving the soil, solid lines indicate processes with estimates of rates and flows. Dashed lines have not been well quantified. dashed lines have not been well quantified. The solid black arrows represent materials (organic matter, nutrients, soil) lost from the soil surface through aeolian processes when dry or via runoff following rain events.

Source: From Collins *et al.* (2014). With kind permission of Annual Reviews.

their initial conditions. The emergence of alternative stable states is typically associated with positive feedbacks that act between ecosystems and environmental drivers at multiple scales (Peters et al. 2004).

8.4.2 Effects of nutrients

There is little doubt that rainfall (or snow in the case of cold deserts such as the Gobi and Great Basin deserts) controls productivity in deserts (Whitford 2002; Chesson et al. 2004). This has often resulted in the assumption that nutrients are unimportant. Whitford (2002) has shown that if the expected rainfall is very low, then nutrient effects may well be low (see also Floret et al. 1982 and Penning de Vries and Djiteye 1982 for perspectives from the Sahara). However, when rainfall is above average, even if only for short periods, then nutrients can indeed be important (Yahdjian et al. 2006; Austin 2011). In low-nutrient ecosystems, such as deserts, rates of nutrient mineralization from organic matter are slow, so nutrient supply and diffusion limit nutrient uptake (Nadelhoffer et al. 1992; Hobbie 2015). Plants from such low-nutrient environments have higher allocation to belowground parts, including mycorrhizae (Cui and Nobel 1992; Collins Johnson et al. 2010), than plants from high-nutrient environments (Chapin et al. 2011). A number of studies have shown that mycorrhizae are important sources of below-ground nutrient allocation, particularly with regard to phosphorus (Bohrer et al. 2008; Collins Johnson et al. 2010; Navarro-Rodenas et al. 2012). However, mycorrhizae cost plants in terms of carbon (Bloom et al. 1985; Wang and Qiu 2006; Bohrer et al. 2008). Besides having traits that increase their ability to take up scarce nutrients, species from low-nutrient ecosystems have inherently low relative growth rates, and thus have a low demand for nutrients (Chapin et al. 2011). This is also the fundamental tenet of the *resource availability hypothesis* of Coley et al. (1985; supported by a meta-analysis by Endara and Coley 2011). That is, plants that live in low-nutrient environments have low growth rates so they cannot afford to lose any photosynthetic or reproductive material. Thus, selection is strong for a defence strategy. Conversely, plants growing in high-nutrient environments can easily regrow any lost material and do not invest as much in defence.

8.4.2.1 Nitrogen

The soil nutrient most often assumed to be important in deserts is nitrogen (Charley and Cowling 1968; Austin and Sala 1999; Austin 2011). Aranibar et al. (2004) found that stable isotopes of soil and plant nitrogen (N) were more ^{15}N enriched in arid than in humid areas in the Kalahari Desert (range of precipitation = 230–930 mm), and the regression relationship was steeper in samples collected during wet than during dry years. This indicates a strong effect of annual precipitation variability on N cycling. Austin and Sala (1999) also found a strong negative relationship between stable nitrogen isotopes and mean annual rainfall in Australia. The correlation of precipitation and ∂^{15}N suggests that annual rainfall input may be an important component controlling ecosystem nitrogen cycling. There are a number of inter-related mechanisms at work that will determine the ecosystem ∂^{15}N signature—a net result of all factors affecting the inputs, outputs, and internal fractionations of ^{15}N over ^{14}N. In addition to the direct effects of precipitation on short-term turnover, long-term losses affecting ecosystem nitrogen pools are reflected in the ∂^{15}N values. The increasingly depleted foliar ^{15}N in wetter sites suggests that, despite potentially more rapid turnover, accumulated losses of nitrogen relative to ecosystem nitrogen pools are greater in the drier sites (Austin and Sala 1999). While the magnitude of both input and output will increase with increasing rainfall, the ratio of loss relative to intrasystem turnover will become smaller, such that increased water availability will result in a systematically less open cycle (Austin and Vitousek 1998). This pattern of decreasing ∂^{15}N with rainfall suggests that the integrated effect of increased rainfall on nitrogen cycling is a decrease in the openness of the cycle itself. What this means is that for every unit of nitrogen that moves through the plant-soil-microbial components of an ecosystem, the potential for loss from that system is greater in sites of lower rainfall (Austin and Sala 1999).

Nitrogen can also accumulate in hyper-arid zones in the absence of biotic turnover from very low rates of N deposition over extended rainless periods (Ewing et al. 2008). Although these fluxes are quite small, the cumulative long-term effect is likely to be substantial. This is especially true if rates of biotic activity are severely inhibited due to extreme conditions of drought or low temperature (Austin 2011). McCalley and Sparks (2009) found that high soil-surface temperatures (greater than 50°C), driven by solar radiation, are the primary cause of nitrogen loss in Mojave Desert soils. Austin et al. (2004) consider that the asynchrony of resource availability, particularly the asynchrony between the availability of nitrogen and water (due to pulsed water events; Weltzin and Tissue 2003), may be key to our understanding of the consequences for ecosystem nutrient retention and long-term effects on carbon and nutrient pools in arid ecosystems.

Ludwig and Flavill (1979) found that primary productivity was reduced in the Chihuahuan Desert (North America) as a consequence of nitrogen limitation, while Floret et al. (1982) found that nitrogen limitation reduced productivity in the Tunisian part of the Sahara during wet periods. In the Sahel in the southern Sahara, Penning de Vries and Djiteye (1982) found that reduced nitrogen availability below a mean annual rainfall of about 200 mm was the source of low productivity. Charley and Cowling (1968) attributed lower productivity in Australian deserts to reduced availability of nitrogen in saltbush desert areas and showed that nitrogen and phosphorus were limiting in central Australian deserts. Friedel et al. (1980) also showed that sulphur could also be a limiting factor in some Australian desert habitats.

In a series of water supplementation–fertilization experiments in the Chihuahuan Desert, a number of studies have shown that nitrogen availability limits biomass production in perennial and annual plants and has an effect on annual plant community composition (Ettershank et al. 1978; Gutierrez and Whitford 1987; Fisher et al. 1988; Gutierrez et al. 1988). However, nitrogen fertilization did not result in changes in productivity in perennial grasses. Irrigation, however, resulted in greater biomass production in the perennial grass, *Bouteloua eriopoda* (Stephens and Whitford 1993). A similar situation was found in the arid Northern Cape province of South Africa for trees (Kraaij and Ward 2006) and for grasses growing there (Mbatha and Ward 2010). In general, nitrogen fertilization and irrigation experiments showed that nitrogen availability affected plant productivity only if moisture availability is high enough for a complete plant growth cycle (James and Jurinak 1978; Romney et al. 1978; Kraaij and Ward 2006; Mbatha and Ward 2010).

8.4.2.2 Nitrogen fixation

Nitrogen fixation may be an important contributor to soil nitrogen in some areas. In the Chihuahuan Desert, Lajtha and Schlesinger (1986) found that *Prosopis* *glandulosa* obtains approximately half of its nitrogen through direct symbiotic fixation. A perennial herb, *Perezia grayi*, had higher levels of nitrogen when growing under *Prosopis glandulosa* than when growing further away or under non-fixing shrubs (*Larrea tridentata*). In the Kalahari Desert, Kambatuku et al. (2013b) found that there was considerable nitrogen fixation by *Acacia mellifera* trees. Furthermore, they found that this occurred when these trees were competing with grasses. When no grasses were present, the trees did not fix nitrogen. This is very similar to the finding of Jacobson et al. (1993) in *Welwitschia mirabilis*, which was not (endo-) mycorrhizal in sites without grasses in the hyper-arid parts of the Namib Desert. In an experimental manipulation, Kambatuku et al. (2013b) found that increasing the level of nitrogen fertilizer led to a decrease in nitrogen fixation by *Acacia mellifera* trees, as might be expected, because there was less need for nitrogen from this source. Schulze et al. (1991) found similar results for *Acacia mellifera* in the Namib Desert. These authors found that nitrogen fixation was associated with reduced intrinsic water-use efficiency. This was particularly noticeable in the arid lowland savannas. However, in another part of the Kalahari Desert, nitrogen fixation associated with trees and shrubs was almost absent in arid areas, even though Mimosoideae (Leguminosae) species dominate (Aranibar et al. 2004). Wiegand et al. (2005) found that nitrogen concentrations under *Acacia reficiens* shrubs were considerably higher than in the surrounding open areas in the Namib Desert, even when the shrubs had died, indicating that this species also fixed nitrogen.

8.4.2.3 Phosphorus

In Australia, phosphorus is also an important nutrient (Orians and Milewski 2007, see the following). Generally, nitrogen and phosphorus are most likely to be important nutrients. Phosphorus is a product of rock weathering while nitrogen comes from an atmospheric pool. Phosphorus occurs in lower concentrations in ancient shield-platform deserts such as the Australian deserts (Orians and Milewski 2007) than in more recent basin and range deserts such as the Great Basin Desert in North America (Whitford 2002). Stafford Smith and Morton (1990) and Orians and Milewski (2007) have stressed the importance of low nutrient availability (especially in phosphorus) in Australian arid systems and have coupled this to the effects of fire. Most Australian soils have 10–440 ppm total P. Samples from arid-zone soils in Australia yielded a mean of 240 ppm total P compared with a mean of 643 ppm total P in arid zones from other continents (Charley and Cowling 1968; Stafford Smith and Morton 1990). Fire is also a prominent feature of the Australian landscape (Stafford Smith and Morton 1990; Creagh 1992; Orians and Milewski 2007). Orians and Milewski (2007) relate the poor nutrients to fire because few animals can consume plants with such poor nutrients, resulting in large amounts of 'expendable energy' to produce well-defended foliage and large amounts of lignified tissues, which leads to intense fires, especially in the spinifex grasslands and mulga (*Acacia*) shrublands. This necessarily assumes a trade-off between growth and defence, although there are many species for which a positive correlation and not a negative correlation has been found (Orians and Ward 2010; Ward et al. 2012). Stafford Smith and Morton (1990) emphasize that many of these features can also be found in other desert regions. However, it is the geographic size of arid Australia, covering 70% of the continent, that makes it so effective an arid region (see also Friedel et al. 1990). This seems somewhat overstated in that there are deserts that are even larger; for example, the Sahara and the Gobi deserts. What might be more important is the proportion of the continent of Australia that is arid is greater than in the Sahara or the Gobi Desert.

8.4.3 Disturbances

There are a number of different types of disturbances that may affect desert ecosystems. Among these, the most important and widespread is probably grazing (Deng et al. 2013; Eldridge et al. 2013). Other disturbance factors include recovering crop lands (physical disturbance) and fire (Suazo et al. 2013; Hulton VanTassel et al. 2015). Another type of disturbance is what Whitford and Kay (1999) termed 'biopedturbation' (soil disturbance by organisms). The contribution of soil disturbance by mammals to heterogeneity is a function of the size and longevity of the soil disturbance. There is a significant positive relationship between longevity of mammal soil disturbance and size of the disturbance: longevity in years = 9.33 $\text{Area}^{0.735}$ (Whitford and Kay 1999). A variety of mammals produce foraging pits that are relatively short-lived and trap plant litter and seeds that are rapidly buried. For example: (1) Boeken et al. (1995) described porcupine diggings in the Negev Desert; (2) Eldridge and Rath (2002) described 'hip holes' created by kangaroos in the Australian deserts; (3) Cuevas et al. (2012) considered wild boar diggings in the Monte desert; (4) Eldridge and Whitford (2014) described the importance of desert rodent disturbances in the Chihuahuan Desert; (5) Ward (pers. obs.) noted Hartmann's mountain zebra, *Equus zebra hartmannae*, wallows in the Namib Desert.

These foraging depressions form nutrient-rich germination sites. High water infiltration rates, a low bulk density rooting environment, and frequently increased soil nutrient content (especially mounds of central-place foragers and larder-hoarders) characterize warren complexes. Productivity tends to be higher on these mounds and the vegetation tends to differ in composition and richness from the surrounding areas. Soil ejected from fossorial mammal burrow systems is generally of low bulk density, erodes readily, and varies greatly with respect to concentration of nutrients and organic matter, depending upon the species and landscape in which the species lives. The variability in soil properties of fossorial burrow system ejecta mounds precludes generalizations about the effects of these disturbances on vegetation. Long-lived features such as nabkhas and heuweltjies are nutrient-rich features that support high productivity and a distinct floral assemblage (Esler and Cowling 1995; Cramer and Barger 2013).

Another source of disturbance is dust (Pointing and Belnap 2014). As mentioned earlier, dust storms can travel thousands of kilometres and can alter non-desert ecosystems. Wind-blown dust may physically damage organisms by scratching the cuticles of plants and insects, leading to increased water loss (Belnap 2003). Dust deposited on plant stomata can reduce photosynthetic rates and even bury seedlings or short plants (Field et al. 2010). Micro-organisms have also been recovered from desert dust and may increase microbial loads in aerosols by as much as ten times (Jeon et al. 2011; Favet et al. 2013).

8.4.4 Decomposition

Many scientists have assumed that water is the primary factor that controls soil processes in arid regions, starting probably with Noy-Meir's (1973) review. The relationship between water availability and other ecosystem processes (as well as in particular soil processes) is much less clear. For example, microbial biomass and activity in deserts is much lower on average than in mesic or humid ecosystems (Fierer et al. 2009a). However, at least two studies have demonstrated that litter decomposition (Martinez-Yrizar et al. 2007; Vanderbilt et al. 2008) does not correlate with seasonal or annual precipitation in deserts, although it is correlated with actual evapotranspiration (Meentemeyer 1978). In addition, in hyper-arid environments, carbon turnover can continue in the absence of rainfall for extended periods of time (Ewing et al. 2008), or during rainless seasons (Dirks et al. 2010). Negative or neutral responses to rainfall inputs suggests that belowground processes have unique controls which are not directly linked to the positive relationship between precipitation and aboveground net primary production (ANPP; Austin 2011).

A major component of decomposition of surface litter in deserts is by the action of termites (Holm and Scholtz 1980; Whitford 2002). Termites may consume up to half the total surface litter and most animal faeces in some deserts. Most materials consumed by termites are completely converted into CO_2 and water because of the action of the symbiotic gut microflora of termites. However, there is a strong *negative* (not *positive*) correlation between termite abundance and soil organic matter (and soil nutrients) ($r = -0.97$) in spite of the fact that soil organic matter and nitrogen are usually positively correlated (Whitford 2002). Thus, little of the litter is converted to soil organic matter, and minerals in litter are returned to the soil in a mineralized state through animal faeces of species that prey on termites, such as lizards and spiders (Whitford 2002).

The process of decomposition of buried litter and dead roots may be very different from that of surface litter (Whitford 2002). Buried litter accumulates moisture, even in relatively dry soils. This consequently lowers temperatures and increases moisture contents, allowing microflora and microfauna to grow. Increasing populations of microflora attract grazers such as protozoans, nematodes, and microarthropods, which attract predators such as predatory nematodes and nematophagous mites (Acari). Complex food webs may be established around moist roots and buried litter. The extracellular enzymes of the microflora rapidly decompose compounds such as sugars, fats, starches, celluloses, and waxes. More complex acid-soluble compounds are slowly attacked by a small subset of microbial heterotrophs (Whitford 2002).

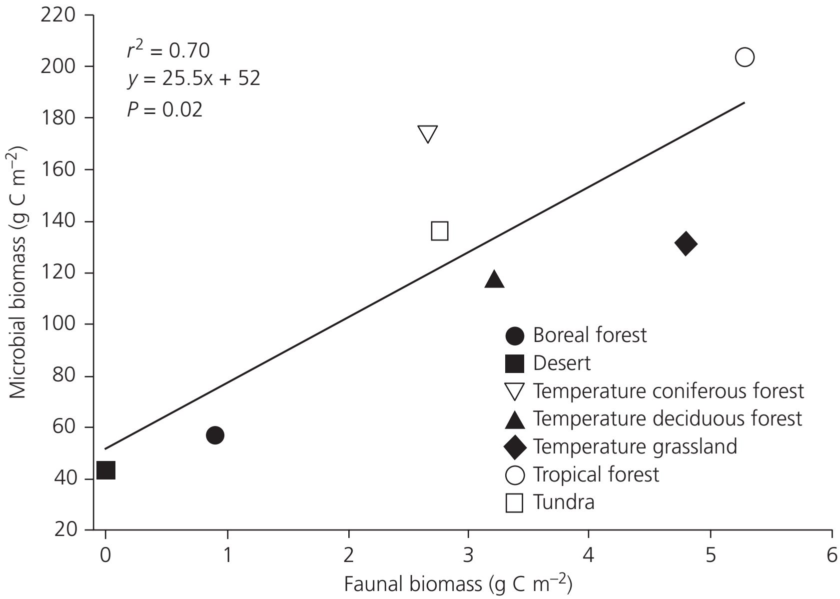

Fig. 8.10 Relationship between soil microbial biomass and faunal biomass across biomes.
Source: From Fierer *et al.* (2009b). With kind permission of John Wiley and Sons.

It is important to note the faunal:microbial biomass ratio was far lower in desert soils (faunal biomass carbon is <0.02% of microbial biomass carbon) than in the other six biomes (Fig. 8.10), where faunal biomass ranged from 1.5 to 3.6% of microbial biomass (reviewed by Fierer et al. 2009b). This may suggest that the desert biome represents a (relatively) more inhospitable environment for soil fauna than for microbes, given that a larger portion of the belowground biomass is microbial. However, a more parsimonious explanation (Fierer et al. 2009b) is that this disparity simply reflects an underestimation of faunal biomass in desert soils because larger fauna were excluded. Larger fauna are likely to be important contributors to desert soil biomass (Petersen and Luxton 1982). Furthermore, Fierer et al. (2009b) excluded fauna residing in deeper soil depths (>25 cm) where desert fauna may be relatively more abundant due to moisture and/or temperature constraints or the limited amount of organic matter on the soil surface (Freckman and Virginia 1989; Lavelle and Spain 2001).

8.4.4.1 Litter breakdown and photodegradation in deserts

Austin (2011) has highlighted the significance of photodegradation of aboveground litter in the decomposition of litter. Photodegradation is the photochemical mineralization of organic matter caused by solar radiation (ultraviolet (UV; 280–400 nm) and photosynthetically active radiation (PAR; 400–700 nm)) (Gallo et al. 2009). Photodegradation leads to the breakdown of cell-wall polymers, releasing gaseous photoproducts of CO_2 and CO, as well as altering the chemistry of the remaining material (Henry et al. 2008; Brandt et al. 2009; Austin and Ballare 2010). In the Patagonian steppe, abiotic photodegradation without biotic interaction was demonstrated to be a dominant control on plant litter decomposition (Austin and Vivanco 2006; Austin et al. 2009). Other experiments showed that reduction in UV-B or total UV radiation decreased decomposition, particularly under dry conditions (Day et al. 2007; Smith et al. 2010), and the attenuation of total solar radiation resulted in reduced mass loss in a range of desert ecosystems (Throop and Archer 2007). This was particularly noticeable in the longer-term study of Vanderbilt et al. (2008), who found no convincing long-term effect of photodegradation with the exception of the breakdown of lignin.

Lignin is an important component of litter quality that is affected by exposure to solar radiation (Day et al. 2007). Most recently, a study demonstrated a mechanistic role for lignin in determining photodegradation rates (Austin and Ballare 2010; see also review by Vanderbilt 2008). Lignin, a well-known inhibitor of biotic decomposition in mesic and humid terrestrial ecosystems, acts as a facilitator of light absorption for photochemical reactions, resulting in mass loss.

8.4.4.2 Heat and wind affect desert decomposition

Desert winds remove carbon and nutrients from these ecosystems but can also transfer microbial populations and extracellular enzymes locally and at larger distances. At a local scale, the direct effects of soil redistribution can affect topography, water redistribution, and albedo, which can affect the landscape heterogeneity of soil processes (Sponseller 2007; Throop and Archer 2007). In addition, there is evidence that soil redistribution could counterbalance the effects of photodegradation due to the burial of litter under shrub patches (Throop and Archer 2007). Soil and litter movement and translocation are common in moisture-limited environments with low and patchy vegetation cover, and litter on the ground is frequently covered to varying degrees with soil and eventually buried (Barnes et al. 2015). This mixing of soil and litter is associated with increased rates of decomposition (Throop and Archer 2007; Barnes et al. 2015). Soil–litter mixing may also buffer litter and resident microbes from the high temperatures and desiccation that commonly occur in hot deserts (Moorhead and Reynolds 1991). These effects could enhance decomposition by extending windows of opportunity for microbial activity following rainfall events (e.g. Cable et al. 2011). Indeed, soil–litter mixing strongly enhanced C mineralization in a laboratory experiment when the soil–litter matrix was subjected to wetting–drying cycles (Lee et al. 2014). The arrival of soil at the litter surface via saltating soil particles or the translocation of litter via overland flow may also promote surface abrasion and increase the surface area available to microbial colonization, leaching, or fragmentation (Throop and Archer 2009; Uselman et al. 2011). Enhanced microbial colonization of recently detached litter may be offset by the negative effects of solar UV on microbes. However, subsequent soil coverage, either as an adhering soil film or as loose soil, could partially and eventually fully shield litter from UV radiation and therefore ameliorate its adverse effects (Cockell et al. 2008; Barnes et al. 2012). Although the mechanisms underlying these soil-mixing effects remain to be fully explored, it is likely that the formation of soil–litter–microbial complexes enhance microbial activity while simultaneously shielding litter from photodegradation (Fig. 8.11).

Clearly, more studies need to be conducted under realistic field conditions to fully explore how solar radiation and soil coverage interact through time to influence litter decomposition in arid ecosystems (Barnes et al. 2015). A conceptual model of the

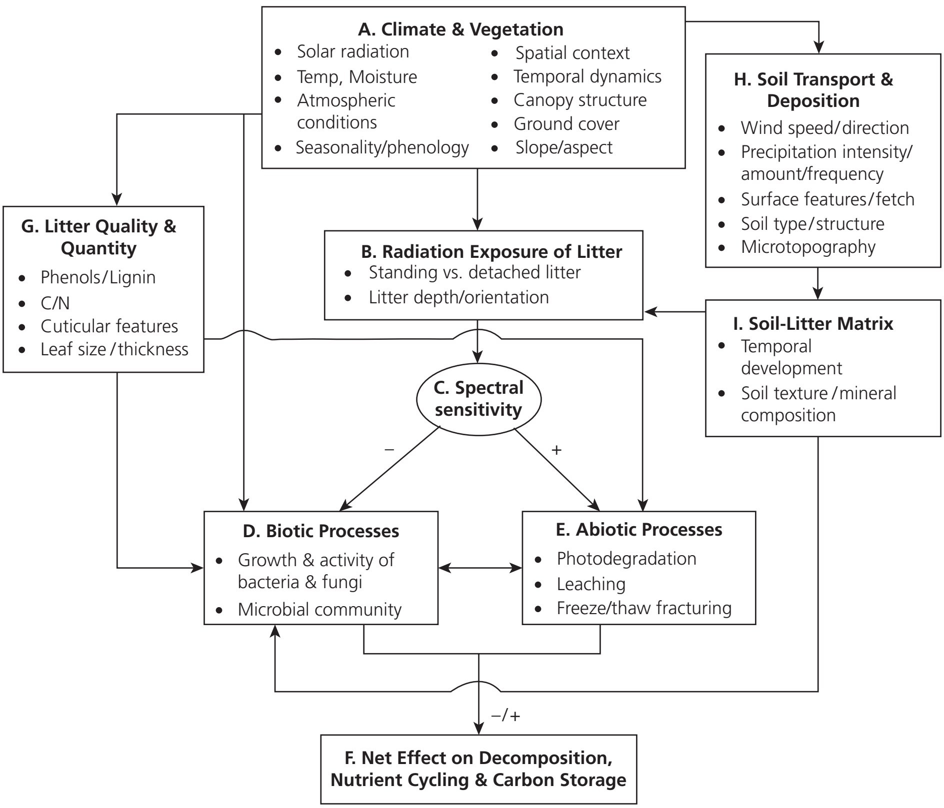

Fig. 8.11 Potential effects of solar radiation (ultraviolet (UV—280–400 nm) and photosynthetically active radiation (PAR—400–700 nm)) and soil–litter mixing on leaf litter decomposition in drylands, including interactions with other environmental factors.

Source: From Barnes et al. (2015). With kind permission of Springer.

interactive effects of soil deposition and sunlight (Fig. 8.12), as proposed by Barnes et al. (2012), may contribute towards resolving the seemingly contradictory findings reported in photodegradation and soil deposition studies.

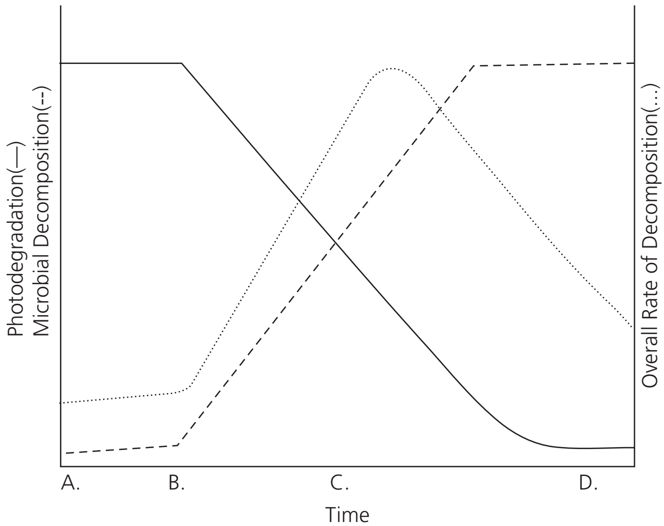

Fig. 8.12 Conceptual model of arid land decomposition following leaf senescence, illustrating the shifting relative importance of abiotic (photodegradation) and biotic (microbial) processes through time and consequent changes in the overall rate of decomposition. Recently senesced plant material is initially subject to high rates of photodegradation while it is standing dead (A). Limited microbial decomposition may then occur on leaf surfaces. While the majority of decomposition that occurs then is from photodegradation, the overall rates of decomposition remain low. When standing dead plant material falls to the soil surface (B), the soil–litter matrix develops, gradually covering the litter (C). During this time the relative importance of photodegradation declines while microbial decomposition increases due to colonization opportunities, favourable microclimate, or abrasion afforded by the litter–soil matrix. Decomposition rates increase with microbial colonization, and overall rates of decomposition peak due to rapid losses of easily decomposable chemical constituents in the litter. Negative effects of UV on microbes are small and transient initially but increase over time in association with increased microbial biomass and activity until soil coverage negates these negative effects. Eventually nearly all the litter surface is cover by soil (D) and photodegradation accounts for a trivial portion of decomposition while microbial degradation prevails. The overall rate of decomposition is low as remaining litter is highly recalcitrant.

Source: From Barnes et al. (2012). With kind permission of Springer.

9 Biodiversity and Biogeography of Deserts

Although there is a common perception that deserts support few species, some deserts have high local diversity, largely because organisms are capable of exploiting patches of high productivity. Here we differentiate between local species richness (also called α diversity), β diversity, which is also known as species turnover or the change in species among sites, and γ diversity, which is regional species diversity. A combination of β and γ diversity is also known as differentiation diversity (Cowling et al. 1999). The size of a region varies considerably, which affects the determination of regional species pools (i.e. γ or regional diversity), because the species–area curve is one of the few 'laws' in nature, which indicates that as area increases, the number of species increases (Arrhenius 1921; Schoener 1989; Pimm 1991; Rosenzweig 1995). Wherever possible, the size of the region being referred to will be indicated.

Productivity–diversity relationships have been well studied in some deserts and have helped us to understand the factors controlling ecosystem function at a large spatial scale. Studies of convergence of desert communities and consideration of the similarity of desert communities with neighbouring mesic communities are some of the best elucidated of this genre. This chapter will also consider the major differences and similarities among desert taxa in the various deserts of the world to draw inferences on the major biogeographic patterns.

9.1 Are deserts species-poor? α, β, and γ diversity patterns

9.1.1 Plants

At the 0.1-ha scale (which is considered α diversity or local diversity scale), some Middle Eastern desert communities in the steppe and true deserts (e.g. Negev Desert) have some of the highest species richness values recorded. In some cases, α diversity can be in excess of 100 species per 0.1 ha (Aronson and Shmida 1992; Ward and Olsvig-Whittaker 1993; Ward et al. 1993). These are mostly annual plants, often belonging to the Poaceae, where there are many relatives of barley *Hordeum vulgarum*, oats *Avena sterilis*, and wheat *Triticum dicoccoides*, as one might expect from the birthplace of modern agriculture (Ward and Olsvig-Whittaker 1993; Ward et al. 1993). These are all winter rainfall deserts. In the Succulent Karoo communities

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of South Africa, species richness can also be very high (mean = 74 species, range = 32–115 species), where most species are dwarf, leaf succulent shrubs (mostly Aizoaceae). Cowling and Hilton-Taylor (1999) consider species presence in the Succulent Karoo to be largely determined by a lottery process (*sensu* Chesson and Warner 1981), where functionally equivalent shrubs coexist in highly dynamic communities. Predictable winter rain and fog-ameliorated summers may provide continuous recruitment, whereas occasional droughts create stochastic conditions for coexistence (Von Willert et al. 1985; Jürgens et al. 1997). The Succulent Karoo has species richness values that are almost double that of the adjacent Nama Karoo (mean = 47 species, range = 22–76 species) (Cowling et al. 1989). The Nama Karoo has values slightly higher than those recorded for Sonoran Desert communities, which were considered by Whittaker and Niering (1975) to be some of the most diverse vegetation in North America.

High β diversity (also called species turnover along habitat gradients, such as rainfall and edaphic gradients) is largely due to habitat specialization and geographic vicariance (Cody 1986; Cowling et al. 1992). In general, this aspect of floral diversity has been poorly studied in drylands (Cowling and Hilton-Taylor 1999). Based on the data from Jürgens (1986) from the Succulent Karoo (South Africa), Cowling et al. (1989) found that there was a compositional shift of 1.5 (using Wilson and Shmida's (1984) β values) for four sites along a gradient of increasing soil depth, spanning only 100 m in horizontal distance in the Knersvlakte (quartz fields) in the Succulent Karoo. Ihlenfeldt (1994) found that there was considerable species turnover in the genus *Argyroderma* (Aizoaceae) in the same area. Thus, in an apparently homogeneous environment, there was exceptional species turnover, based largely on edaphic changes (Ihlenfeldt 1994). Similar patterns of species change have been recorded for other genera of Aizoaceae (Hammer 1993; Schmiedel and Jürgens 1999) as well as geophytes (Goldblatt and Manning 1996; Esler et al. 1999). Comparatively speaking, β diversity in the adjacent Nama Karoo of South Africa is low (Cowling and Hilton-Taylor 1999). Hoffman (1989) recorded a species turnover of 1.9 for four sites along a 250-km gradient of increasing aridity, from succulent thorn thickets (mean annual rainfall = 450 mm) to karroid shrubland (mean annual rainfall = 200 mm). Also in the Nama Karoo, Palmer and Cowling (1994) recorded β diversity values of 1.1 and 1.5 for five sites spanning topo-moisture gradients of 500 m and 300 mm year^{-1} on dolerite and sandstone substrates. Cowling and Hilton-Taylor (1999) consider species turnover in the Succulent Karoo to have occurred explosively within certain lineages (e.g. Aizoaceae; Klak et al. 2004; Valente et al. 2014), which has resulted in the coexistence of many related species separated by very short distances.

In terms of regional data for arid habitats, Cowling et al. (1998) found that winter-rainfall arid lands have more plant species than summer-rainfall arid areas, when measured globally (almost twice as species-rich as equivalent summer-rainfall areas). When compared with winter-rainfall areas, the Succulent Karoo (which is in a winter-rainfall area) has the highest regional diversity (nearly four times as high as in similar-sized areas of North America). The Namib Desert has between two and four times as many species as the Sahara in North Africa, despite the greater topographic complexity of the latter region (Cowling et al. 1998).

9.1.2 Animals

Because most deserts are recent in their distributions, many species are (convergently) derived from mesic faunas (Morton 1993). There are also some interesting patterns of certain species from the arid regions of northern and southern Africa that are the same species (or closely related) yet are separated by savanna, grassland, and forest, which indicates that they were once contiguously distributed prior to the Pleistocene (Fig. 9.1).

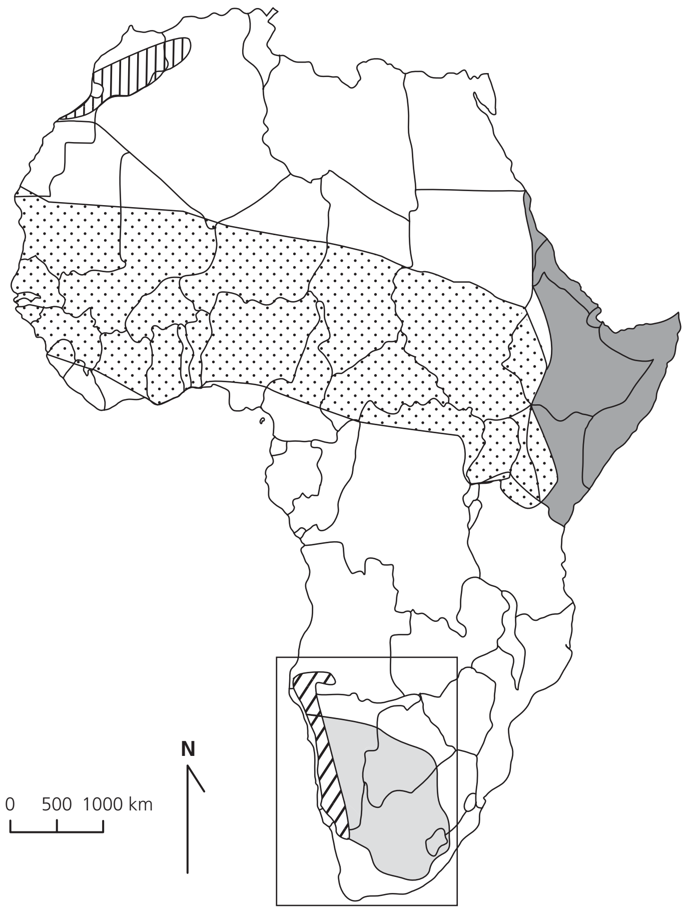

Fig. 9.1 Map of the distribution of the small mammal *Xerus*, which is a desert genus found in deserts of northern and southern Africa (see Chapter 4), yet is not found in areas in between. The areas between these deserts are dominated by savanna, grassland, and forest. Hatched = *X. princeps*, grey = *X. inauris*, black = *X. rutilus*.

Source: From Herron et al. (2005). With kind permission of University of Chicago Press.

9.1.2.1 Lizards

The regional lizard fauna (γ diversity) in the deserts of Australia is richer than the lizard fauna of North American deserts (170 vs 57 species) (Schall and Pianka 1978), even though deserts are very similar in size on these continents (about 8 million km^2; Westoby 1993). Local diversity (α diversity) in Australia is also richer (mean of 30 species) on average than in North American deserts (mean of 7 species). Pianka (1969) proposed a number of reasons for the greater diversity of Australian desert lizard species:

1. In Australian deserts, lizards replace the North American desert species of mammals.
2. Some Australian desert lizards are more narrowly specialized than their North American equivalents, for example, the skink genus *Ctenotus*.
3. As a consequence of the greater environmental stability of the Australian deserts, lizards have been able to partition their niches both spatially and temporally. For example, there are virtually no nocturnal North American gecko species versus 32–44% in Australia.
4. There is greater environmental heterogeneity of the Australian deserts than their North American counterparts. However, the low topographical variety of Australian deserts (Stafford Smith and Morton 1990; Orians and Milewski 2007) would militate against this argument.

Morton and James (1988) considered why subterranean lizards are absent from North American deserts, yet are quite common in Australian deserts. Subterranean lizard species are also common in the Kalahari Desert (southern Africa) (Huey et al. 1974). Similar to Pianka (1986), Morton and James (1988) considered ecological factors to be of greater importance than other factors in explaining higher present-day diversity in Australia. Lizards are quite diverse in many arid parts of the world, probably because the costs of thermoregulation are lower in arid areas and they can become inactive during stress periods, which confers an advantage for them over endotherms (birds and mammals), which must feed on a daily basis. Among the most diverse habitats for lizards are the spinifex grasses (*Triodia* and *Plectrachne*) (Fig. 9.2). Pianka (1972) and Cogger (1992) consider that the spiny nature of these grasses makes predation on lizards very difficult, the microclimate is probably less harsh than the microhabitats at large, and there is horizontal structural diversity within spinifex. Pianka (1981) also considered spinifex hummocks to provide a rich insect supply. Morton and James (1988) show that termites are particularly abundant in spinifex grasslands because spinifex is low in nutrients (as indicated by its sclerophylly). These insects are primarily subterranean, which may explain why there are so many subterranean lizard species.

James and Shine (2000) have more recently moved the focus away from local-scale explanations of lizard diversity and have attempted a regional analysis. They used the Australian comb-eared skinks of the genus *Ctenotus* and found that more species occur in the arid zone (9.3 species per site) than in other biomes in Australia (means = 2.4 to 7.6). Pianka (1969) found that as many as 11 species of *Ctenotus*

Fig. 9.2 Spinifex (*Triodia* spp.) grasslands in the Strzelecki desert, South Australia.
Source: Photo used under a Creative Commons licence.

occur sympatrically. Pianka (1969) considered ecological coexistence to occur on the basis of differences in body size, foraging time, microhabitats, and habitats (see also Morton and James 1988). However, James and Shine (2000) found that the total number of species occurring in the arid zone is actually lower, not higher, per unit area of habitat than other biomes in Australia. Thus, although xeric *Ctenotus* have a higher α diversity than mesic species of Australia, they have a lower γ (regional) diversity. This occurs because most xeric species occur over enormous areas (average = 1,035,000 km^2), whereas their congeners have smaller geographic ranges (200–373,000 km^2). The enormous geographic distributions of xeric taxa probably reflect the spatial (especially topographic) homogeneity of desert regions of Australia (see Chapter 8). This means that the sizes of geographic zones of individual species are large, which leads to greater probabilities of evolutionary radiation (Schluter and Ricklefs 1993). Thus, in contrast to the patterns of other taxa, significant radiation has occurred within the xeric regions, rather than radiation within the mesic regions with subsequent radiation into the massive desert zones. James and Shine (2000) recognized that biological attributes regarding interactions with other species or with other resources (e.g. shelter or prey) may still be important at microhabitat scales (Pianka 1986; Morton and James 1988).

9.1.2.2 Granivores

Presence–absence data for the small mammal species at sites in seven deserts were analysed for evidence of similarity in community structure (Kelt et al. 1996). The deserts studied by Kelt et al. (1996) were in North and South America, Australia, the Middle East, and greater Eurasia (including the Thar, Turkestan, and Gobi deserts). They found that there was low α diversity (2–4 spp. per site), high β diversity (i.e. high species turnover or many changes across sites) and local coexistence of 20–30% of species in terms of γ (regional) diversity. Although there were some similarities across deserts, trophic structure differed considerably. Deserts in the northern hemisphere (especially in North America) had more granivores and the Turkestan Desert had more folivores. Carnivorous small mammals were particularly abundant in Australia, and omnivores were common in Australia, the Thar Desert of India, and South America. They found that the structure of the small mammal communities in deserts was strongly affected by historical factors. Different taxa with distinct trophic adaptations were common in different deserts.

Morton and Davidson (1988) considered the diversity of arid Australian and North American harvester ant faunas. Because there are fewer rodents in Australia than in North America, they predicted that harvester ants should be more diverse. They found that there was similar α diversity between the deserts but that there was higher β diversity in Australia. The species richness in North American deserts ranged from 2 at lower rainfall to a maximum of 8 at higher rainfall, whereas in Australia, species richness ranged from 6 to 12 harvester ant species. Richness and diversity were significantly correlated with mean annual precipitation in North American deserts but there was no significant relationship in Australia. Consequently, Australian deserts had higher species richness at low rainfall than North American deserts (<300 mm rainfall). As mentioned in Chapter 7, granivory is an important interaction in ecological communities, especially in deserts where many plant populations exist as seeds for long periods (Davidson and Morton 1981; Morton 1985; Rissing 1986). Harvester ants have been shown, in a number of deserts (Australia, South Africa, and South America), to be the most important granivores and seed dispersers (Morton 1985; Kerley 1991) (Fig. 7.16), although rodents are more important in North American and Israeli deserts (Mares and Rosenzweig 1977, 1978; Abramsky 1983). Fox (2011) has shown that there is no dominance of trophic use of a single resource among small mammal species across continents. In South America there are 58% herbivores, in South Africa there are 52% omnivores, North America has 50% granivores, Australia has 49% insectivores, and Eurasia has roughly equal proportions of granivores, herbivores, and omnivores (about 30% each)(Table 9.1). Seed availability shows substantial overlap across regions, with greater maxima in North America, but is unlikely to be the sole explanation for greater granivory in that continent. Fox (2011) notes that granivory appears to be less important in deserts that experience disturbances, which may be related to the reduced reliability of seed resources (the emphasis here is on the variability in seed resources and not the average availability). Fire, droughts, rainfall, and extreme climatic events such as El Niño (or ENSO) can affect resource pulses, which in turn control the degree of disturbance. Ants, in contrast, seem less affected by fluctuations in seed availability because of their greater ability to store seeds that offsets periods of reduced seed availability (Fox 2011).

Table 9.1 Proportions of granivores in different deserts

Region	% Granivores
North America	50
Eurasia	31
South America	4
Southern Africa	11
Australia	3

Source: From Fox (2011).

9.1.2.3 Birds

Wiens (1991) found no evidence that local bird species diversity (α diversity) differed between Australian and North American desert shrublands, at a scale of about 10 ha. In both cases, there were about six species for any given shrubland. Pianka and Huey (1971) found the species richnesses of Australian and Kalahari (southern Africa) deserts to be similar, despite the great differences in size (Australian deserts are far larger). These similarities in species diversity may be a consequence of association of bird species diversity with vegetation structural diversity rather than productivity per se (MacArthur and MacArthur 1961; Recher 1969; Pianka and Huey 1971; Cody 1970, 1993). Pianka and Huey (1971) found that about 63% of the variance in bird species richness could be explained by variance in plant height diversity. Because structural diversity of the three deserts is relatively similar, there may be little opportunity for more species to occupy different niches. Kaphengst and Ward (2008) found that bird species composition but not species richness or diversity was affected by vegetation structural diversity in the arid Northern Cape province of South Africa. They found that there was a strong positive correlation between bird species richness and maximum vegetation height in these plots. A similar conclusion was reached by Sirami et al. (2009). When Kaphengst and Ward (2008) removed all of the encroaching *Acacia mellifera* shrubs from ten 1-ha plots, the birds occupying those plots changed from predominantly aerial insectivores such as drongos and bee-eaters to primarily cursorial birds such as larks and pipits.

Overall, regional species diversity (γ diversity) is quite similar between Australian deserts (140 species (excluding water birds)) and North American deserts (130 species) (Schall and Pianka 1978; Morton 1993). Pianka and Huey (1971) compared avian functional diversity in the Kalahari Desert (southern Africa) with western Australian deserts. They found that there were proportionately more ground carnivores (including insectivores) in the Kalahari Desert (34%) than in Australia (18%), that avian ground herbivores (mostly granivores) were similar on the two continents, and that there were more arboreal Australian species (53%) than in the Kalahari Desert (38%).

9.1.2.4 Animals in ephemeral pools

Ward and Blaustein (1994) studied arthropod diversity in ephemeral pools in the Negev Desert (Israel) (Fig. 9.3). They found that while species–area relationships could explain some of the variance in species richness, more of the variance could be explained by the amount of vegetation in these pools. Overall, flash floods caused pools to return to their original state and for the colonization process to start afresh. In this case flash floods were by far the overriding factor determining arthropod diversity in ephemeral pools.

Regardless of the potential overriding effects of time since inundation described by Ward and Blaustein (1994), there are clearly also biotic effects that are important for inhabitants of ephemeral ponds. For example, Walton (2001) studied the association between a size-selective floodwater predator, the tadpole shrimp (*Triops newberryi*), and aspects of the aquatic insect community (successional pattern, size structure, and composition) in replicate ponds in the arid Coachella Valley of southern California. Walton (2001) found that the abundance of early colonists, particularly the mosquito (*Culex tarsalis*), chironomid larvae, and mayfly nymphs, and the size structure of the aquatic insect communities in ponds containing tadpole shrimps differed significantly from ponds without shrimps. Based on headwidths of co-occurring aquatic insects, ponds containing tadpole shrimps at densities >5 individuals m^{-2} had fewer small instars of aquatic insects relative to ponds without *Triops*. The composition of aquatic insect communities in ponds containing tadpole shrimps differed from ponds without *Triops*, particularly during the first 3 weeks

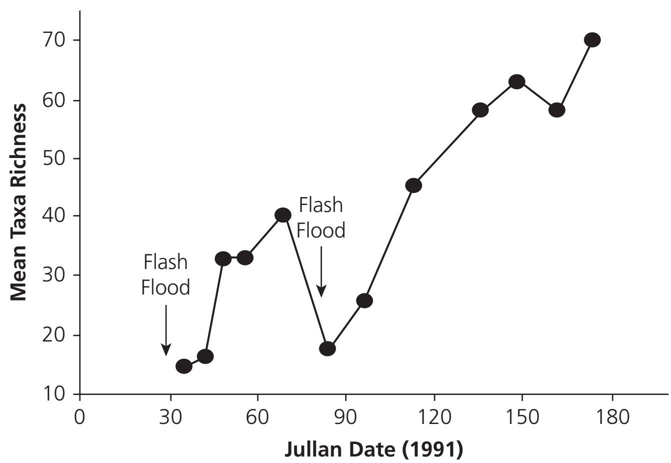

Fig. 9.3 Ward and Blaustein (1994) studied arthropod diversity in ephemeral pools in the Negev Desert (Israel) and found that, while species:area relationships could explain some of the variance in species richness, flash floods caused pools to essentially return to their original state and for the colonization process to start afresh.

Source: From Ward and Blaustein (1994). With kind permission of Blackwell.

after flooding of these pools. Similarly, Starkweather (2005) found that isolated rock pools in the arid desert near Las Vegas, Nevada, often develop dense populations of a rock-dwelling species of the rotifer *Hexarthra*. Starkweather (2005) found that rotifers persisted in these isolated ponds due to the absence of predation by adult fairy shrimp (*Branchinecta mackini*), which is the dominant anostracan in this region in these winter ponds. In most cases, individual female (but not male) fairy shrimp consumed the smaller rotifers.

An interesting case of a perennial desert well, called Montezuma Well, with unusual aquatic invertebrate dynamics occurs in the Sonoran Desert of Arizona (Ellsworth and Blinn 2003). This well has nearly constant thermal conditions (mean 21.1 ± 4°C) and very little variation in nutrient conditions (Blinn et al. 1994). The zooplankton community in Montezuma well is quite simple, consisting of high densities of the endemic filter-feeding amphipod *Hyalella montezuma* and the cyclopoid copepod *Tropocyclops prasinus mexicanus. Tropocyclops prasinus mexicanus* has a bimodal pattern of abundance with peaks in mid-summer and mid-winter. Continual reproduction, rapid egg development, and abundant food explain the high summer densities of *Tropocyclops prasinus mexicanus*. Boucher et al. (1984), during a four-year study, reported that phytoplankton densities in the well were nearly five times higher during the summer than during the winter. The reason for the winter peak is less clear, although Ellsworth and Blinn (2003) note that the conventionally filter-feeding amphipod *Hyalella montezuma* can be an effective predator/omnivore. In winter, *Hyalella montezuma* is almost absent due to declines in the availability of phytoplankton, leading these authors to suggest that predation by *Hyalella montezuma* allows *Tropocyclops prasinus mexicanus* to increase in abundance (they record having seen *Tropocyclops prasinus* in the maxillae of *Hyalella montezuma*).

9.2 Productivity–diversity relationships in deserts

Ward and Olsvig-Whittaker (1993) and Ward et al. (1993) considered the Makhtesh Ramon as the junction of two major biogeographical zones, the Saharo-Arabian and the Irano-Turanian. They found that there was a single productivity curve based on rainfall that increased species richness with increasing rainfall. This was different from the result achieved by Ghazanfar (1991) in the desert of Oman, where a hump-shaped curve was obtained (Fig. 9.4). Rosenzweig and Abramsky (1993) would argue that Ward and Olsvig-Whittaker (1993) had sampled only a portion of the hump-shaped curve; that is, they had sampled the low productivity portion of the curve, which is correct. The declining portion of the curve would have been at higher productivity.

Abramsky and Rosenzweig (1984) found that there was a hump-shaped species diversity curve for Negev Desert rodents (Fig. 9.5), as predicted by Tilman (1982) and also by Newman (1973). Similar patterns were found in the Sonoran and Gobi deserts by Rosenzweig (1995). They considered the reason for the increase in the

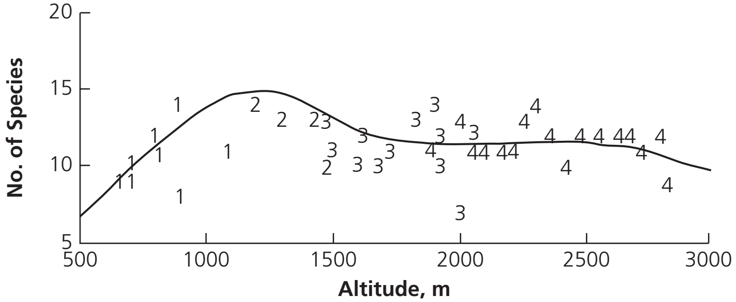

Fig. 9.4 Ghazanfar (1991) obtained a hump-shaped species richness versus altitude curve for flowering plants in the desert of Oman. Numbers are the four ecological zones indicated by the clustering programme, TWINSPAN.

Source: From Ghazanfar (1991). With kind permission of Blackwell.

hump-shaped diversity curve to be rather clear (Rosenzweig and Abramsky 1993). The curve increases initially because as productivity increases, more species can occupy a particular habitat. This is most probably a function of environmental heterogeneity. Rosenzweig and Abramsky (1993) find it more difficult to explain why the number of species declines after a certain point. It is commonly thought that this decline is a function of competition among species for resources (Newman 1973; Tilman 1982). However, Rosenzweig and Abramsky (1993) questioned whether this explanation for the decline phase is tautological. They argue that habitat and resource heterogeneity are *evolved* responses of organisms and find no a priori reason why more species can evolve into any particular variance rather than a smaller particular variance. That is, they wonder why species could not have evolved changes that might not develop in ecological time.

9.3 Convergence and divergence of desert communities

One of the main differences between floras and faunas of the world, particularly in deserts, occurred because of the break-up of Pangaea (Wegener 1966) and the later split between the southern Gondwanan continent (which formed South America, Antarctica, Africa, Australia, and India) and the northern Laurasian continent (which formed North America and Eurasia). For example, the hemiparasites of the family Loranthaceae are mostly Gondwanan in origin, although some movement into adjacent areas has occurred (e.g. the invasion of the Negev Desert (Israel) by the mistletoe *Plicosepalus acaciae* from Africa; Fig. 9.6). Similarly, there has been a divergence in the origin of desert birds, because the South African, South American, Indian, and Australian species are Gondwanan in origin, whereas the North American and Eurasian species are Laurasian in origin (Cracraft 1973; Schodde 1982). This is particularly true of the mostly flightless ratite birds (Palaeognathae), which are found in South

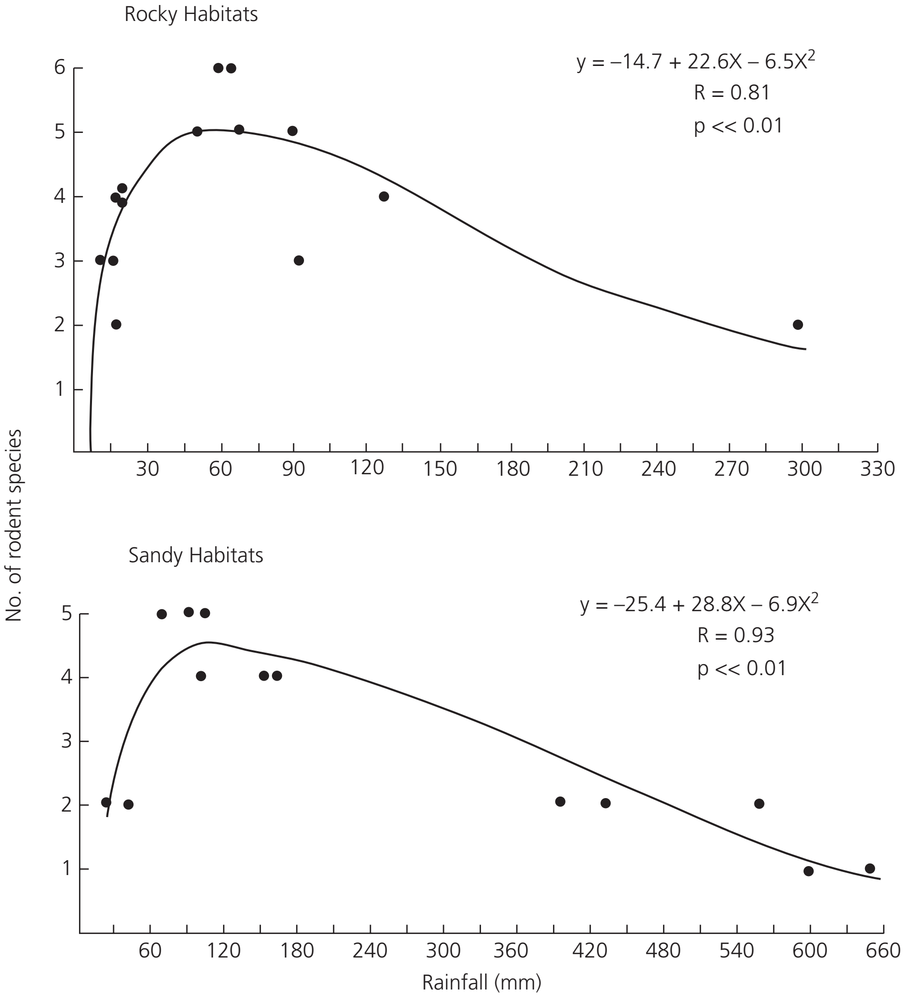

Fig. 9.5 Abramsky and Rosenzweig (1984) found that there was a hump-shaped species diversity curve for desert rodents.

Source: From Abramsky and Rosenzweig (1984). With kind permission of Nature Publishing Group.

America (rhea and tinamou—tinamous are the only ratites that can fly), South Africa (ostrich), Australia (emu, cassowary and kiwi), and the fossil elephant bird (*Aepyornis maximus*) in Madagascar and the fossil moa (*Dinornis giganteus*) in New Zealand (Baker et al. 2014; Mitchell et al. 2014). This has led to a great interest in panbiogeography and vicariance biogeography (*sensu* Croizat 1962, 1982; Cracraft 1973). However, a puzzling example is the absence of the Solifugae (sun spiders) from Australia and their presence elsewhere in historical Gondwana (Fig. 9.7).

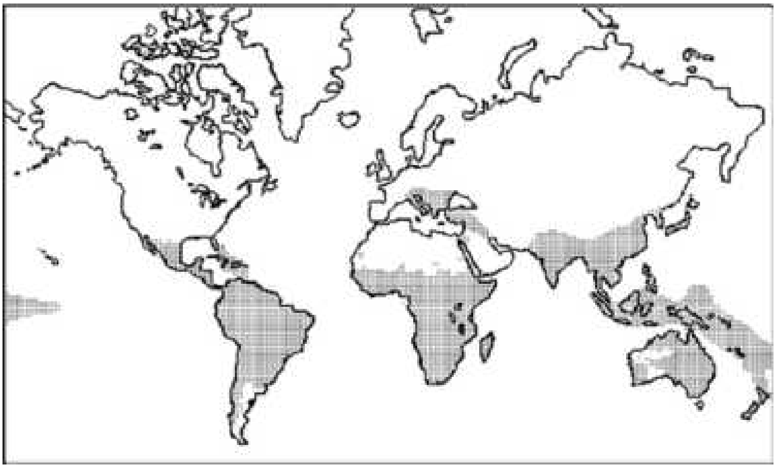

Fig. 9.6 Gondwanan distribution of Loranthaceae.

Source: From http://parasiticplants.siu.edu/Loranthaceae/. Date accessed 22 February 2016.

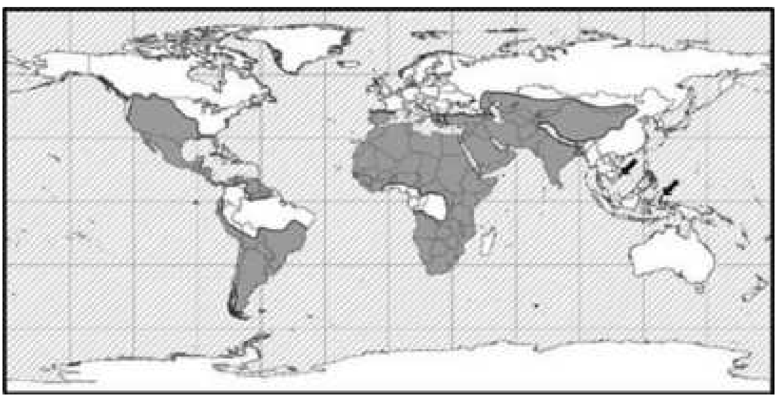

Fig. 9.7 The absence of the Solifugae (sun spiders) from Australia, which was also a part of Gondwana, is hard to explain.

Source: From http://www.solpugid.com/GSIS%20Diversity%20Inventories.htm. Date Accessed 22 February 2016.

Perhaps more interesting are the cases of convergent evolution of desert forms, presumably because of the similarities in selection pressures placed on these organisms. The classic example of convergence is the succulent Cactaceae in the Americas and the Euphorbiaceae in Africa, as is the convergence of stem-succulent tree aloe and stem-succulent *Yucca* (Fig. 9.8). The Aizoaceae (Plate 9) and Crassulaceae (in Africa; Van Ham and Hart 1998; Mort et al. 2007, 2009), Moringaceae (in Africa (Fig. 9.9) and Asia; there are only 12 species in this monotypic family (Olson 2010), 9 of which

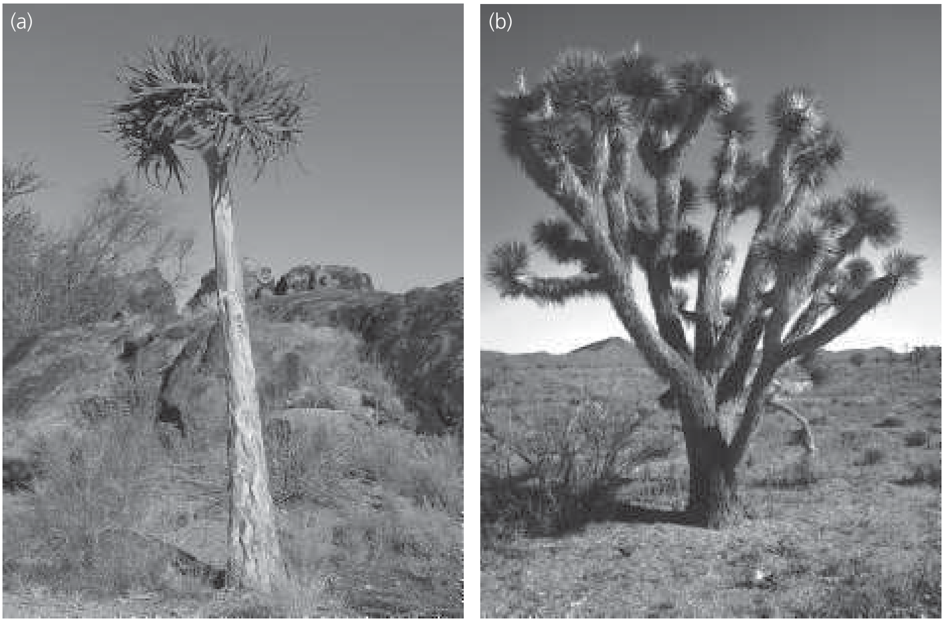

Fig. 9.8 The classic example of convergence is the stem-succulent Cactaceae in the Americas and the stem-succulent Euphorbiaceae in Africa. Another pertinent example is the *Aloe* genus in South Africa (a) and *Yucca* genus (b) in North America.

Source: Photos under Creative Commons licence.

occur in the arid Horn of Africa and 8 of these are endemic to this region), and Didiereaceae (arid regions of Madagascar; Applequist and Wallace 2000) are also strongly succulent desert taxa.

The deserts of North and South America are remarkably similar from a floristic point-of-view. Almost all of the large desert families (Asteraceae, Polygonaceae, Zygophyllaceae) and many genera are shared by the two continents (Raven 1963). Although some have claimed that this similarity was due to long-distance dispersal (Raven 1963; Solbrig 1973; Wells and Hunziker 1976) or the short distance that colonization needs to occur across the Isthmus of Panama, Turner (1977) has suggested that North and South America were geographically closer in the Early to Mid-Tertiary (about 65 million years ago), resulting in the great similarity between their floras. However, the families Agavaceae, Cactaceae, Oenotheraceae, Garryaceae, Krameriaceae, Lennoaceae, and Polemoniaceae are almost exclusively restricted to the Americas and have not dispersed to other arid regions (Turner 1977). Furthermore, the lack of similarity in North and South American mammalian faunas is surprising (see section 9.4.2 'Animals').

There are also similarities among freshwater organisms found in deserts. Whitford (2002) has indicated that many of the same genera of freshwater pool (ephemeral)

Fig. 9.9 Moringa *ovalifolia* from arid Namibia.
Source: Photo from Violet Gottrop under Creative Commons licence.

fauna inhabit ponds throughout the world. Many of the Anostraca, Conchostraca, Notostraca, and Cladocera found in the Sahara Desert are of the same genera as found in North American deserts (Rzóska 1984; Mackay et al. 1990; Maeda-Martínez 1991; Daniels et al. 2004). However, Whitford's (2002) conclusion was likely based on the limited capabilities of morphological analyses. For example, Witt et al. (2006) found in the Great Basin Desert that a 'morphologically difficult' aquatic taxon *Hyalella* (Amphipoda) to classify was readily differentiated into many cryptic species using DNA barcoding. For example, 33 cryptic species formerly ascribed to *Hyalella azteca* were recognized. These authors recognize that there is no explicit species concept (Coyne and Orr 2004). Furthermore, Ebach and Holdrege (2005) and Meyer and Paulay (2005) note that the delineation of DNA-barcoded species may be fairly arbitrary. In their defence, Witt et al.

(2006) note that they used a highly conservative criterion for differentiating DNA-barcoded species that was about ten times the norm.

Daniels et al. (2004) have examined the phylogeny and distribution of the thermophilic genus *Streptocephalus* (Streptocephalidae, Anostraca) in North America, Africa, Eurasia, and Australia using molecular techniques. They found that there was considerable homoplasy in morphological characteristics (Maeda-Martínez 1991; Hamer et al. 1994a, b). Daniels et al. (2004) have found that the North American taxa are monophyletic and that none of these taxa has a close relationship with any of the other members of the genus. They believe that the distribution patterns of the genus *Streptocephalus* are best explained by vicariance during the break-up of the supercontinent of Gondwana. Only a single dispersal or vicariant event is needed to explain the monophyly of the North American species from Gondwana. Daniels et al. (2004) note that there is a faunistic link for a number of Gondwanan freshwater crustacean taxa between Africa and Australia and also with India (which was also a part of Gondwana) (Newman 1991).

There are also fascinating examples from desert rodents shown by Mares (1983), although more recently he has recognized that morphological similarity is not necessarily associated with trophic similarities. Kelt et al. (1996) found that the claims of convergent evolution in small mammal faunas (Mares 1983) to be spurious in that the mammals may look similar but occupied different niches. Mares (1983) has indicated that bipedal rodents such as the Heteromyidae of North America (Hafner and Hafner 1983; Schmidly et al. 1983) and Dipodoidae of Asia (Pisano et al. 2015) are perceived to be granivorous. However, there is no link between bipedality and seed eating (Meserve et al. 2011a). In fact, bipedal rodents may also be herbivorous, omnivorous, or insectivorous (Kelt et al. 2015). Thus, morphological convergence is not necessarily linked with granivory.

9.3.1 Community-wide character displacement

Ecological character displacement may occur when any two or more species overlap in a crucial aspect of their niches (Eadie et al. 1987). This may lead, in time, to morphological changes that differentiate the species into different niche use. Ward (2009) considered the size-distribution patterns of tenebrionid beetles (also called darkling beetles) in the Namib Desert belonging to the genus *Onymacris* (see also Roberts et al. 1991; Ward and Seely 1996a–c). Although it may be difficult to assign competitors to any given pair of species, Ward (2009) assigned any pair of species that occurred either sympatrically (i.e. occurred together) or allopatrically (i.e. occurred separately), based on their presence or absence in quarter-degree square units. He found that that the differences in body lengths of beetles was greater for beetles that occurred sympatrically than allopatrically, inferring that interspecific competition could have occurred (Fig. 9.10).

Dayan et al. (1989) studied two foxes in the Saharo-Arabian Desert, and included the data for a third species where it occurs. One species, the red fox (*Vulpes vulpes*),

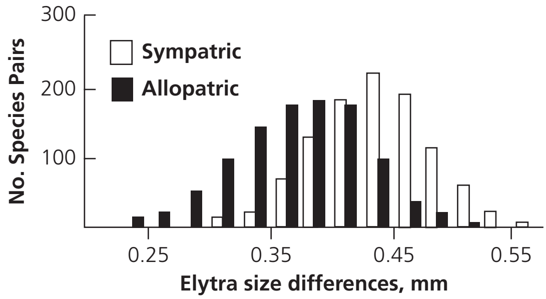

Fig. 9.10 Sympatric *Onymacris* beetle species were significantly more different in size than allopatric species.

is widespread in the Holarctic, whereas the smaller Rüppell's fox (*Vulpes ruepellii*) is restricted to the deserts. The third species, Blanford's fox (*Vulpes cana*), is smaller than the other two species and is also restricted to deserts. They found that the carnassial teeth of these species were remarkably evenly spaced in size (Fig. 9.11) in the deserts where they are sympatric in spite of the general indication that the

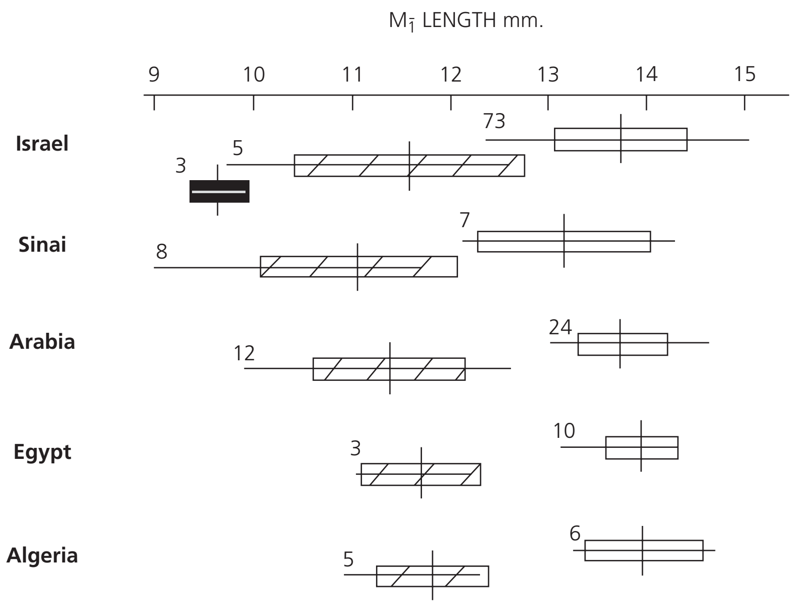

Fig. 9.11 Dayan et al. (1989) found that the lower carnassial tooth lengths of these foxes were remarkably evenly spaced in size in the deserts where they are sympatric. Vertical lines: means; bars: 2 standard deviations; and horizontal lines: range. Empty bars = red fox; dashed bars = Rüppell's fox; black bar = Blandford's fox.

Source: From Dayan et al. (1989). With kind permission of Blackwell.

red fox follows Bergmann's rule (i.e. increases in size as one travels northwards; Bergmann 1847; Clauss et al. 2013). The only area where the red fox does not follow Bergmann's rule is where it is sympatric with Rüppell's fox. They understood this to indicate that ecological character displacement has occurred to limit the size similarity of these species.

In a series of studies, Martin and Pfennig (2009, 2011) and Pfennig and Martin (2010) found interesting patterns of disruptive selection and character displacement in two species of spadefoot toads, *Spea multiplicata* and *Spea bombifrons*, in ponds in the Sonoran Desert of the southwestern United States. Martin and Pfennig (2009, 2010) showed that disruptive selection occurred in *Spea multiplicata*. They showed that selection favoured extreme trophic phenotypes over intermediate individuals. They also showed that disruptive selection reflected ecological specialization as well as resource competition—extreme phenotypes foraged more effectively on the main alternative resource types, and the intermediate phenotypes, which are often the most common phenotype, compete more with each other than with extreme forms. The intensity of disruptive selection increased with conspecific density (Fig. 9.12). In allopatric populations of *Spea multiplicata* and *Spea bombifrons*, both species produce omnivorous and carnivorous morphs. In sympatry, *Spea multiplicata* produce only the smaller omnivorous morph and *Spea bombifrons* only the larger carnivorous morph (Pfennig

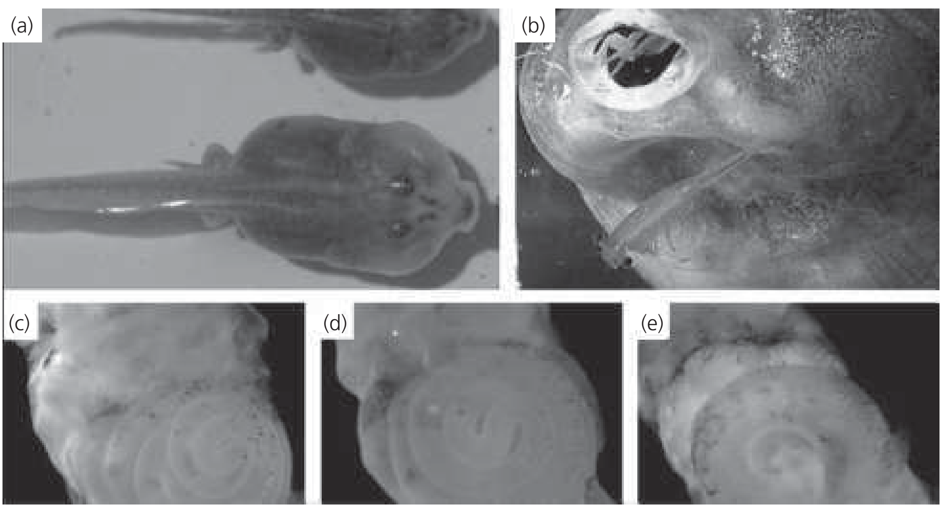

Fig. 9.12 Omnivorous *Spea multiplicata* is a smaller morph than the carnivore (a). Many ponds also contain an intermediate form between these two types. Intermediate individuals are selected against because they feed less effectively than either of the two extreme forms on detritus (omnivore) and fairy shrimp (carnivore). Carnivores (b) have a notched beak and large jaw muscles to enable to feed more effectively on fairy shrimp. Additionally, the omnivore has a longer gut to better digest detritus (c) than the intermediate morph (d) which, in turn, has a longer gut than the carnivorous morph (e).

Source: Photo from Martin and Pfennig (2009). Kind permission of University of Chicago Press.

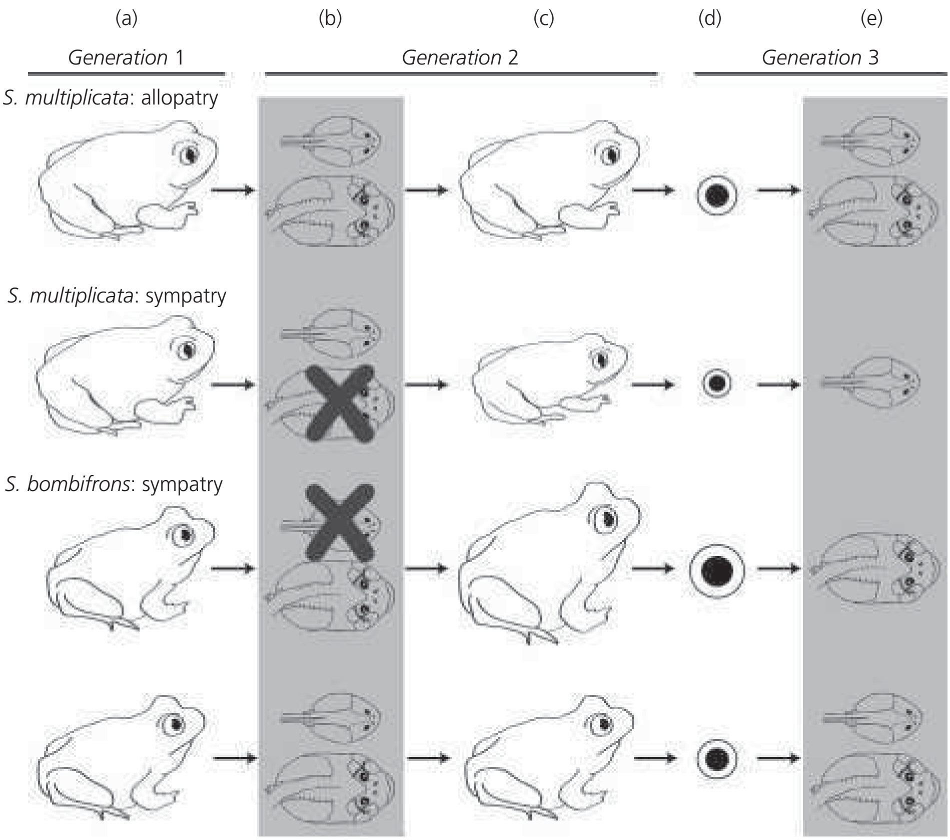

Fig. 9.13 Transgenerational epigenetic inheritance can mediate character displacement in spadefoot toads. (a) Two of these species (*Spea multiplicata* and *Spea bombifrons*) occur in allopatry and sympatry (middle rows) with each other. (b) In allopatric populations, both species produce an omnivore morph and a larger, shrimp-eating carnivore morph. When the two species first came into contact, phenotypic plasticity allowed them to diverge in morph production, such that one species (*Spea multiplicata*) produced mostly omnivores, whereas the other species (*Spea bombifrons*) produced mostly carnivores. (c) Because *Spea multiplicata* produce both morphs in allopatry, but only the smaller omnivore morph in sympatry (*Spea multiplicata* is a poorer competitor for shrimp than *Spea bombifrons*), *Spea multiplicata* females from sympatry are smaller and in poorer condition when they mature than *Spea multiplicata* females from allopatry. By contrast, because they produce both morphs in allopatry but only the larger carnivore morph in sympatry, *Spea bombifrons* females from sympatry mature larger and in better condition than *Spea bombifrons* females from allopatry (the carnivore morph is larger because it is able to monopolize the more nutritious shrimp resource). (d) Consequently, in sympatry, the two species diverge in maternal investment: *Spea multiplicata* females invest less into offspring by producing smaller eggs, whereas *Spea bombifrons* females invest more into offspring by producing larger eggs. (e) Smaller eggs (egg size is indicated by circles) hatch into smaller tadpoles, which tend to become omnivores. By contrast, larger eggs hatch into larger tadpoles, which tend to become carnivores. Thus, by the third generation following contact with a competitor species, each species may be 'epigenetically' canalized to produce an alternative morph. Eventually, the two species accumulate genetic differences: sympatric populations are genetically fixed for producing a single morph, which is distinct from that produced by the other species.

Source: From Pfennig and Servidio (2013). With kind permission of De Gruyter.

and Martin 2010; Martin and Pfennig 2011). Pfennig et al. (2015) also tested whether sexual selection played a role in the differentiation of the two morphs. However, they found that this effect, while present, was much less than the effect of ecological specialization and resource competition. Pfennig and Pfennig (2012) and Pfennig and Servedio (2013) proposed that transgenerational epigenetic inheritance was responsible for character displacement in these two spadefoot toad species (Fig. 9.13).

9.4 Large-scale patterns in desert biogeography

Crisp et al. (2001) considered the factors that have led to endemism in the Australian flora. Crisp et al. (2001) found that, as is the case for other taxa (with the exception of the lizards; see Chapple and Keogh (2004) and section 9.4.2, 'Animals'), the expansion of mesic species into the adjacent xeric areas has occurred, largely because the present position (and age) of deserts is relatively recent. Crisp et al. (2001) found that all centres of endemism are near-coastal, which they consider to be associated with Pleistocene expansions of the central deserts, which limited the viability of refugia for narrowly endemic species. Africa has also been well studied with regard to endemism (White 1993; Linder 2000). Linder (2000) found that climate stability rather than high rainfall was correlated with areas of endemism. He found that expansions of the desert during past arid cycles (Pleistocene, 10,000–20,000 years BP) have removed sources of endemism, even in apparently suitable areas such as mountain ranges. Indeed, the deserts were probably connected during the Pleistocene for different periods, leading to similarities in taxa and even shared species such as birds (Vernon 1999). Nonetheless, Burke (2004) has shown that patterns of plant endemism in various parts of the world differ considerably (Fig. 9.14).

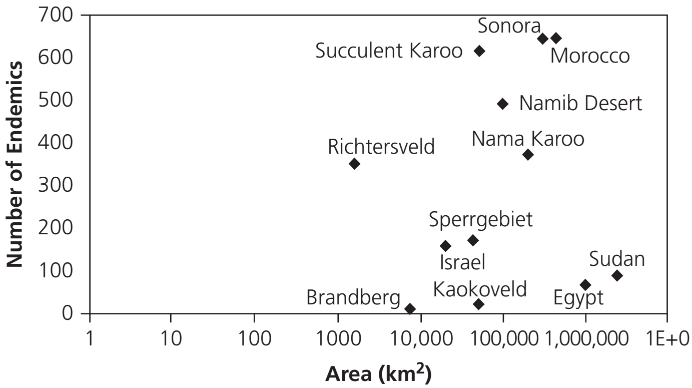

Fig. 9.14 Burke (2004) has shown that patterns of plant endemism in various parts of the world differ considerably. Sperrgebiet, Brandberg, and Kaokoveld are in the Namib Desert (Namibia), Richtersveld is part of the Karoo (South Africa).

Source: From Burke (2004). With kind permission of Blackwell.

9.4.1 Plants

The various desert regions of the world have been divided by Shmida (1985) into nine phytogeographical regions based on the similarities in their floras (Fig. 9.15 and Table 9.2): (1) Australian; (2) Southern African; South American deserts, namely (3) Monte-Patagonian and (4) Atacama-Sechuran; (5) Sonoran; (6) Artemisian (Great Basin); (7) Irano-Turanian; (8) Sahelian; and (9) Saharo-Arabian.

In the Old World of the Northern Hemisphere, there is general agreement that there are three phytogeographical regions (Shmida 1985):

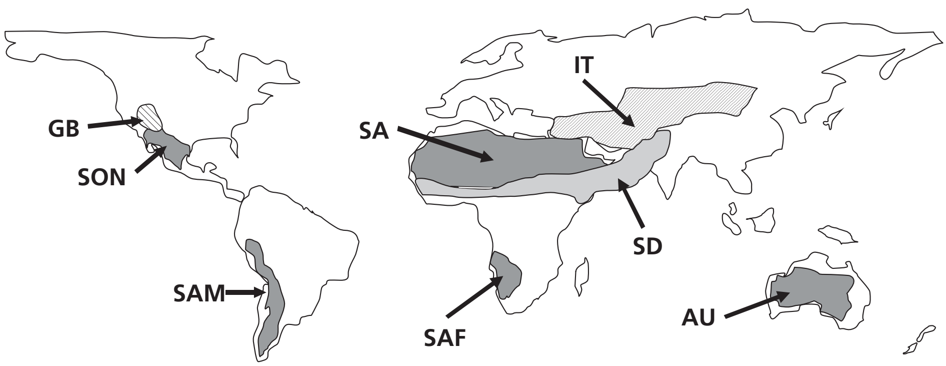

Fig. 9.15 Map of Shmida's (1985) desert phytogeographic regions of the world. AU: Australia; GB: Great Basin; IT: Irano-Turanian; SA: Saharo-Arabian; SAF: southern African; SAM: South American (includes Monte-Patagonian and Atacama-Sechuran); SON: Sonoran; SD: Sudano-Decanian.

Source: From Shmida (1985). With kind permission of Elsevier.

Table 9.2 The main plant families expressed as a percentage of species richness of some desert regions of the world

Plant families	Australia	South Africa	Irano-Turanian	Arabian	Sahara	Thar	North America	World
Acanthaceae						2.7		
Agavaceae							1.0	
Aizoaceae	1.4	15.0			*2.1			*1.0
Amaranthaceae						2.4		
Asclepiadaceae		2.0						1.5
Asteraceae	23.2	20.2	11.6	14.0	11.0	6.4	19.3	11.1
Boraginaceae			4.3	3.8	2.3		4.6	
Brassicaceae	3.2		10.4	5.6	3.2		4.0	
Cactaceae							*2.8	*0.1

Continued

Table 9.2 (*Continued*)

Plant families	Australia	South Africa	Irano-Turanian	Arabian	Sahara	Thar	North America	World
Capparidaceae					2.3	1.4		
Caryophyllaceae			4.6	5.4	2.6			
Chenopodiaceae	*11.6	2.7	*7.9	*7.4	*3.4	*1.0	*2.4	*0.7
Convolvulaceae						5.6		
Crassulaceae		*5.6	1.8					*0.7
Cucurbitaceae						3.2		
Cyperaceae								1.8
Epacridaceae	**1.8**							
Euphorbiaceae		2.3				3.4		2.6
Fabaceae	9.2	4.0	7.9	7.4	10.7	14.0	6.1	7.6
Fouquieriaceae							0.1	
Geraniaceae		2.9			1.4			
Goodeniaceae	**3.2**							
Hydrophyllaceae							3.1	
Iridaceae	3.3							
Lamiaceae			2.7	3.0	1.7			2.0
Liliaceae	2.2	8.3	2.4	4.8				
Loasaceae							2.2	
Malvaceae	1.9					4.6		
Melastomataceae								1.7
Myoporaceae	**1.6**							
Myrtaceae	**5.0**							
Onagraceae							2.2	
Orchidaceae								7.8
Oxalidaceae		1.5						
Poaceae	11.4	6.4	13.8	8.2	11.1	15.0	7.0	4.0
Polygonaceae			3.0				4.9	
Polemoniaceae							4.1	
Plumbaginaceae					1.8			
Proteaceae	1.8							
Rosaceae			2.4					
Rubiaceae								3.3
Scrophulariaceae		5.2	2.6			2.4	2.8	1.8
Solanaceae	2.4							
Zygophyllaceae	1.6	*2.3		*3.0	*2.8	*2.3		*0.1

*= desert family. Exclusively desert families indicated in bold.

Source: After Shmida (1985). With kind permission of Elsevier.

1. Irano-Turanian, including the Iranian and central Asian deserts (Walter 1973);
2. Saharo-Arabian, which includes the deserts of the Sahara and Arabia. Surprisingly, the deserts of the Irano-Turanian (cold) and Saharo-Arabian (hot) regions differ in temperatures but are highly similar floristically; and
3. Sahelian (also known as Sudano-Deccanian; Zohary (1973)), which includes the Thar (Great Indian) Desert. This region also includes the arid savanna south of the Sahara. The last-mentioned is interesting, with taxa such as *Acacia* species, *Capparis decidua, Indigofera, Maerua, Moringa, Salvadora persica, Ziziphus*, and many members of the grasses (Poaceae) being shared with the arid savanna of Africa.

Shmida (1985) recognizes only one Australian desert region. However, in a more recent analysis, Gonzalez-Orozco et al. (2014) have examined the phytogeography of Australia and recognize some further subdivisions of Australian deserts. The north–south split between the Eremaean and Northern Desert Region (Fig. 9.16) roughly coincides with the Tropic of Capricorn and the summer–winter rainfall line. Previous biome descriptions, proposed in the Australian Bioregionalization Atlas (ABA), and defined by both climate and biota (Burbidge 1960; Beard and Goodall 1976; Beard 1981), identified a large arid Eremaean region that is not split north to south into two regions as was found in the Gonzalez-Orozco et al. (2014) analysis. Gonzalez-Orozco et al. (2014) provided evidence that suggests that the division line between Eremaean and Northern Desert regions might be related to the effect of the Tropic of Capricorn, which may have resulted from the palaeoclimatic shifts (warmer-cooler-warmer) during the past 65 million years (Zachos et al. 2001). Gonzalez-Orozco et al. (2014) also observed a west–east climatic division within the Eremaean and Northern Desert regions (Fig. 9.15). Gonzalez-Orozco et al. (2014) also found that there was little overlap with the regional diversity of Australian desert animals.

The classification of Linder et al. (2012) also differed from the classification of Shmida (1985) in that they consider that there are several deserts in sub-Saharan Africa, based on their analyses of plants, mammals, birds, and amphibians. Consistent among their analyses of the various taxa were the presence of a Somali desert zone as well as a Namib desert zone. Linder et al. (2012) also found that some taxa indicated that there was an adjacent Ethiopian semi-arid zone.

The environments of the Sahel and the Thar regions are similar but they are separated by the Indian Ocean. Shmida (1985) considered that there was a connection of arid savanna via Saudi Arabia and southern Iran as long-distance dispersal and the Gondwana connection (India split off from Africa about 85 million years ago) seem unlikely because the similarity in genera and species (i.e. indicating recent speciation) is too great. Many Sahelian species occur in the mountains of Yemen and Oman (Zohary 1973). Long-distance dispersal may, of course, have caused the dispersal of species from Africa to India across the Red Sea and Gulf of Oman, which is a distance of 50–200 km.

The interesting case of dispersal of *Acacia raddiana* was considered by Shrestha et al. (2002) as an example of the similarities between desert areas of Africa and Asia. Shrestha et al. (2002) have shown that mammalian dispersal significantly affects and,

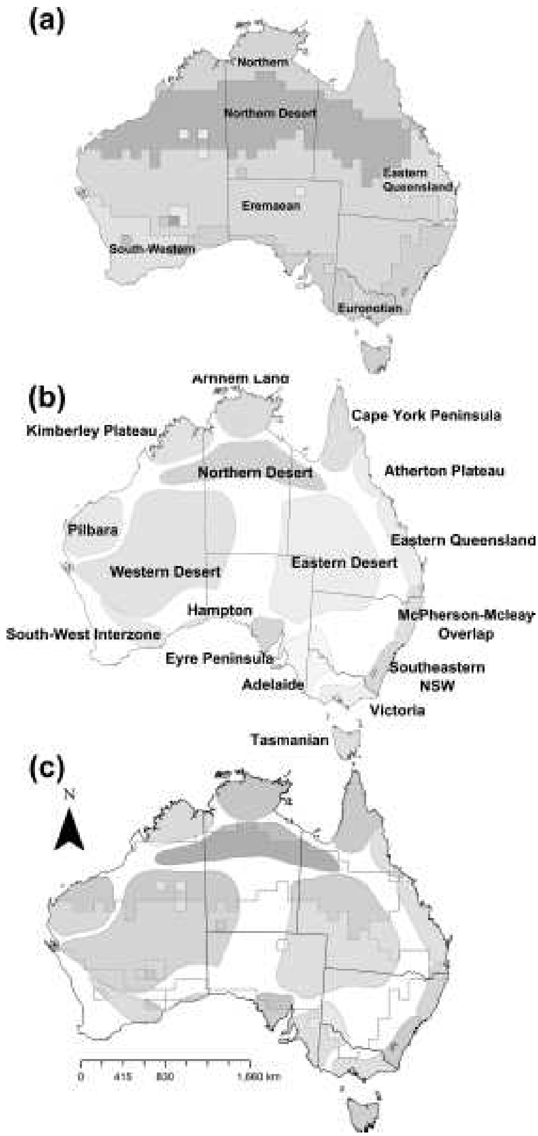

Fig. 9.16 Spatial agreement between (a) Gonzalez-Orozco et al. (2014) phytogeographical regions of Australia and (b) the Australian Bioregionalization Atlas (ABA). (c) The degree of spatial overlap among each of the Gonzalez-Orozco et al. (2014) and ABA regions.

Source: After Gonzalez-Orozco et al. (2014.) Published in *PLoS One* under Creative Commons licence.

indeed, controls the biogeography of *Acacia* trees in the Middle East on a large geographic scale. Shrestha et al. (2002), using randomly amplified polymorphic DNA (RAPD) analyses, showed that there are two main genetic groups of *Acacia raddiana* trees in the Negev Desert, one in the western Negev, extending to the northern shores of the Dead Sea, and the other along the Syrian-African Rift valley from the Red Sea to the southern end of the Dead Sea (Fig. 9.17). As these trees have large, heavy seeds that need to be scarified prior to germination (which occurs easily in the guts of large herbivores; Rohner and Ward 1999), they must have been dispersed from Africa (where the main populations of this species are found) by mammalian herbivores across the flat expanses of the western Negev Desert to the northern Dead Sea. Independently, seeds must have been carried from south to north in the Syrian-African Rift valley from the Sinai (Egypt) and/or Saudi Arabia and up the wadis (ephemeral rivers) entering the valley by large mammals as water-borne transport of seeds in the west–east running wadis cannot account for the upward movement of seeds in the wadis or the north–south directionality in *Acacia raddiana* genetics.

Some perplexing differences between the Sahara and the southern African deserts occur. There are only eight true desert species shared between the Sahara and the Namib, for example (Werger 1978). The deserts differ considerably in their dominant taxa. The Chenopodiaceae (e.g. *Anabasis, Haloxylon, Artemisia, Calligonum, Ephedra*, and *Retama*) are dominants in the Sahara but are missing from southern African deserts, whereas the Aizoaceae, Amaryllidaceae, Crassulaceae, and Iridaceae (all of which are succulents or geophytes) are very poorly represented in the Sahara and dominant in the Namib (Shmida 1985; Esler et al. 1999). This may be because the Namib in particular has been a desert for such a long time (*c*.55–80 million years; Ward et al. 1983), whereas the Sahara has only been a desert for a maximum of about 7 million years (Schuster et al. 2006). Interestingly, the gymnosperm genera *Ephedra* (Sahara) and *Welwitschia* (Namib) are now considered to be members of the Ephedraceae in the tribe Gnetales (Price 1996; Jacobson and Lester 2003).

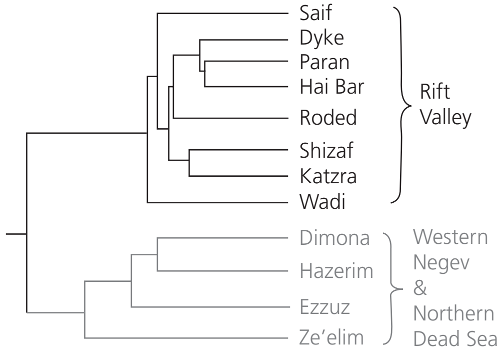

Fig. 9.17 Cluster analysis of *Acacia raddiana* populations in the Negev Desert, Israel.
Source: From Shrestha et al. (2002). With kind permission of Elsevier.

There are a number of geophytes with flattened leaves that lie prostrate on the soil surface in the Succulent Karoo of South Africa (Esler et al. 1999) (Fig. 9.18). At least eight families (Amaryllidaceae, Colchicaceae, Eriospermaceae, Geraniaceae, Hyacinthaceae, Iridaceae, Orchidaceae, Oxalidaceae) contain prostrate-leaved geophytes. Although this growth form occurs infrequently through the summer-rainfall temperate regions of Africa, it is virtually absent in other regions in the rest of the world. However, the growth form is relatively common in many geophyte lineages in the Succulent Karoo biome and the Cape mediterranean zone (Fynbos biome), also known jointly as the Cape Floral Kingdom (Esler et al. 1999). One might argue that it has evolved from the adjacent fynbos, which is the world's most species-rich biome. However, this does not appear to be the case. A number of reasons have been postulated to explain this. Esler et al. (1999) believe that the mild winter temperatures and low variability in annual rainfall are key features for the presence of these geophytes in South Africa.

Schmiedel and Jürgens (1999) worked in the Knersvlakte, which is a quartz field region of the Succulent Karoo, South Africa. They also found very high local species diversity (52 quartz field specialist species), many of which were endemic species (39 species), with many belonging to the subfamily Mesembryanthema (Aizoaceae). Quartz fields supported many tiny, nearly globose, succulent chamaephytes, with convergent growth patterns being demonstrated in two genera *Argyroderma* and *Gibbaeum* (both Aizoaceae). Schmiedel and Jürgens (1999) believe that there is restricted competition from larger growth forms, which are incapable of growing in shallow soils of such low nutrient value and high soil salinity. Similar to Esler et al. (1999), Schmiedel and Jürgens (1999) believe that the mild winter temperatures and low variability in annual rainfall contribute to the success of these tiny chamaephytes. With regard to the biogeography of *Argyroderma* on the Knersvlakte, Ellis

Fig. 9.18 Prostrate-leaved geophytes, *Brunsvigia* sp., from the Succulent Karoo (Namaqualand), South Africa.

and Weis (2006) and Ellis et al. (2006) used transplant experiments to demonstrate that there were survival advantages for species that remained in their home sites relative to those that were switched between sparse and dense quartz habitats as well as between microenvironments within the dense quartz habitat. Ellis and Weis (2006) suggested that divergence between *Argyroderma* species occupying different edaphic microenvironments probably results from local adaptation (i.e. genotype by environment ($G \times E$) interactions; see also Chapter 11), with coexistence facilitated by response to fine-scale habitat variation (Fig. 9.19).

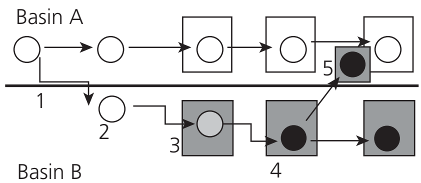

Fig. 9.19 Schematic diagram of radiation in genus *Argyroderma*. There are five stages proposed by Ellis et al. (2006): (1) Colonization of spatially isolated drainage basins. (2) Neutral genetic divergence as a result of restricted gene flow between basins. (3) Adaptive phenotypic divergence if the predominant edaphic environments differ between drainage basins. (4) Flowering time shifts associated with morphological changes in different habitats. (5) Range expansion on the same habitat resulting in coexistence of previously isolated taxa differentiated along habitat use and flowering time axes. Stages listed here are indicated by numbers on the diagram.

Source: From Ellis et al. (2006). With kind permission of Blackwell.

The Ellis et al. (2006) example of local adaptation in *Argyroderma* indicates that evolution occurs by natural selection. However, evolution does not only occur by natural selection. For example, Gorelick (2009) has suggested that the evolution of the cacti (Cactaceae) has occurred largely by genetic drift. He indicates that, due to polyploidy (resulting in reticulate evolution; Majure et al. 2012), inbreeding, and endemism, effective population sizes of individual cactus species were small, leading to random genetic differences among populations. According to Gorelick (2009), this frequently led to speciation. He particularly notes the development of the cephalium (Fig. 9.20), which is at the base of the inflorescence in certain genera of the Cactaceae. The cephalium appears to have no apparent function, or at least had a different function in the past, i.e. *exaptation* (Gould and Vrba 1982). Gorelick (2009) also argues that genetic drift is high in the Cactaceae on the basis of evidence for high linkage disequilibrium. Among the reasons for high linkage disequilibrium cited by Gorelick (2009) is the small effective population sizes of many cactus species. However, this could also be due to genetic hitchhiking (A. Verboom, pers. comm.). Much of Gorelick's (2009) argument is based on the opposite of Gould and Lewontin's (1979) criticism of adaptationist thinking, 'The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist program', where it was assumed that any characteristic was an adaptation, regardless of how obscure that might be (cf. cephalium). However, the fact that everything is not an

Fig. 9.20 Cephalium of *Melocactus melanzanus*.
Source: Photo by Stan Shebs, under a Creative Commons licence.

adaptation does not mean that nothing is an adaptation. Furthermore, using the argument of small effective population size at the present does not mean that it has always been so. It is possible that genetic drift and other random genetic differences may have led to evolutionary change in the Cactaceae, but there are lots of examples of adaptive change, such as in the evolution of succulence in this largely arid lineage (e.g. Ogburn and Edwards 2010; Arakaki et al. 2011) and the evolution of determinate primary root growth in arid Cactaceae and its absence in non-arid forms of this family (Shishkova et al. 2013). Arakaki et al. (2011) argue that there were major radiations of succulent lineages, including Cactaceae (Barcenas et al. 2011), Euphorbiaceae (Evans et al. 2014), ice plants (Mesembryanthema; Klak et al. 2004; Valente et al. 2014), and agaves (Good-Avila et al. 2006) between 10 and 5 million years ago, which was consistent with a major reduction in the concentration of carbon dioxide in the atmosphere. Reduced CO_2 would have made water stress more extreme in arid environments, producing a substantial advantage for succulent plants and promoting their radiation across the landscape. Whether there was subsequent genetic drift that resulted in radiation as suggested by Gorelick (2009) bears further investigation.

The two most widespread families in deserts are the Chenopodiaceae and the Zygophyllaceae (Shmida 1985). Some genera, for example, *Artemisia* of the Asteraceae, are widespread in North America and in the Sahara and Arabian deserts, yet are absent from the southern African deserts. Among the 154 genera that Thorne (1973) listed as subcosmopolitan, about a quarter are halophytes (including the Chenopodiaceae and Tamaricaceae). Perhaps, once ecomorphological adaptation to extremely salty habitats occurred, there is a higher probability of long-distance dispersal over ocean barriers than salt adaptation occurring *de novo* on another continent (Shmida 1985). Interestingly, the four most important desert families (Aizoaceae, Chenopodiaceae, Portulacaceae, and Zygophyllaceae) are succulent or have members that are succulent (Shmida 1985; Cowling and Hilton-Taylor 1999).

Psammophilous (sand and dune) plants show a distribution similar to that of the halophytes. For example, in the Middle Eastern deserts, at least a few psammophilous genera (and species), such as *Artemisia monosperma* (Asteraceae), *Pancratium* (Amaryllidaceae), *Danthonia, Panicum*, and *Stipagrostis* (all Poaceae), grow both in deserts and in coastal sands (Danin 1996). A transitional group consists of halophilous–psammophilous taxa (e.g. *Tamarix nilotica* and *Zygophyllum album*) that grow on salty sand in the Sahara and near the Mediterranean coast.

9.4.2 Animals

The situations with animals are more complex than with flowering plants (angiosperms) and gymnosperms (e.g. *Welwitschia* (Namib Desert) and *Ephedra* (Saharo-Arabian deserts)). For example, the Solifugae (sun spiders) are found across the deserts of the world, with the exception of Australia. Conversely, the genera of invertebrates of ephemeral pools are largely shared across the world's deserts (Whitford 2002). This section will focus on a single taxon, the small mammals, which are rather well known.

There are distinct lineages of desert-dwelling small mammals. Most notable are the Australian taxa, which are mostly marsupials. The largest group of marsupial mammals is the Dasyuridae (e.g. *Antechinomys, Dasyuroides, Sminthopsis*). There are murid (Muridae) lineages in Australia, including two of the most species-rich genera, *Notomys* and *Pseudomys* (Kelt et al. 1996). Asian deserts are dominated by the Muridae and the Dipodidae (Pisano et al. 2015), although there is no overlap of murid genera with those of Australian deserts. The Asian desert murids include the gerbils (Gerbillinae: e.g. *Dipodillus, Gerbillus, Meriones, Tatera*) and the dipodids (represented by *Allactaga, Jaculus*, and *Cardiocranus*) (Pisano et al. 2015). Pisano et al. (2015) present evidence that the Dipodoidea had a Himalayan origin. North America has the endemic family Heteromyidae, including the kangaroo rats (*Dipodomys*) and pocket mice (*Perognathus*) (Hafner and Hafner 1983; Alexander and Riddle 2005). The Heteromyidae are unique in that they have external fur-lined cheek pouches, which may be unique for specializing on seeds (Mares et al. 1997). North America also has a number of genera of cricetine rodents (Cricetinae). In South America, there are caviomorphs (e.g. *Octodon* and *Octodontomys*) and the more recent but more diverse cricetine group, including the genera *Akodon, Auliscomys, Eligmodontia*, and *Phyllotis*. Thus, each desert has relatively distinct lineages, with no overlap in genera (Kelt et al. 1996).

As indicated earlier, these taxa have evolved from mesic ancestors, on the periphery of the deserts. In North America, pluvial/interpluvial periods plus the presence of seed-specialized heteromyid rodents have led to the importance of granivory at both the local and regional scales (Heske et al. 1994). In contrast, the low relief and extensive area of the central Asian deserts (Gobi and Turkestan deserts) and the Australian deserts have not produced frequent isolation between populations, and so have not favoured extensive speciation (contrast this with the extensive radiations of Australian lizards; Morton and James 1988). This topography has favoured small mammalian species with large geographic ranges and rather low β diversity (Shenbrot et al. 1994). The arid regions of Australia have produced mostly omnivores and carnivores, which may reflect phylogenetic conservatism because dasyurid marsupials are mostly carnivorous and conilurine rodents are mostly omnivorous (Kelt et al. 1996). However, the Thar Desert (India) is relatively small and is bounded by forested areas. This desert is largely anthropogenically derived (due to heavy human pressures) and is conspicuous for its absence of desert-adapted species (Prakash 1974).

The South American deserts show clear dominance by omnivores and folivores at both local and regional scales (Marquet 1994; Meserve et al. 1996, 2011b). There are no water-independent species in South America, strict granivores are few, and carnivory is restricted mostly to the marsupial *Thylamys elegans* (Meserve 1981). The difference in species' diversities between the Sonoran Desert (North America) and Monte Desert (South America) is remarkable, given their proximity (Mares et al. 1977). There are a number of major differences in the two mammalian faunas as a whole, based on analyses of a single site each:

1. Three orders (Artiodactyla, Lagomorpha, Insectivora) occur in the Sonoran Desert and do not occur in the Monte Desert.
2. The order Edentata (e.g. armadillo) is absent from the Sonoran Desert.
3. Bat and rodent species in the Sonoran Desert are about twice as common as in the Monte Desert. There are 20 species of bats and 14 rodent species in the Sonoran Desert versus 9 species of bats and 8 species of rodents in the Monte Desert (Mares et al. 1977).

Mares et al. (1977) found that both α and β diversities (at a single site in the Sonoran and Monte deserts) are higher in the Sonoran Desert of North America than in the Monte Desert of South America. It is possible that the contraction and expansion of arid intermontane basins with each pluvial and intervial phase (Schmidly et al. 1983) have resulted in greater opportunities for allopatric speciation in North America (especially of heteromyid rodents) than in South American deserts. Glacial cycles seem to have affected South America less strongly than in the northern hemisphere (Clapperton 1993).

Kelt (2011) notes the need to better understand the composition of small-mammal assemblages. Clearly, local diversity is necessarily constrained by the species pool that can potentially colonize the area (Wiens and Donoghue 2004), which includes the constraint that those small mammals must be adapted to the harsh desert conditions

(Shenbrot et al. 2010). Kelt (2011) believes that it is necessary to employ data from long-term studies to understand the features that are key to assemblage structure. The only long-term study that fits this criterion is the study conducted by J.H. Brown and colleagues in the Chihuahuan Desert at Portal, Arizona, U.S.A. This study was initiated in 1977. The kangaroo rats *Dipodomys* species were excluded from a number of replicate sites by means of small gates (Ernest et al. 2008). No other rodent species replaced the kangaroo rats for many years and there was no compensation in use of energy resources by the remaining small mammals. However, Bailey's pocket mouse (*Chaetodipus baileyi*) immigrated into the site in 1996, some 18 years later. Historical records show that *Chaetodipus baileyi* was neither widespread nor abundant near Portal (Ernest and Brown 2001a). The nearest habitat patches known to have *Chaetodipus baileyi* in them before initiation of the kangaroo rat removal in 1977 were 15 km from the study site (Ernest et al. 2008). This demonstrates the constraint placed on local species diversity by the species pool (Thibault et al. 2004; Kelt 2011). Within a few years, *Chaetodipus baileyi* was taking up to 90% of the food resources previously consumed by the *Dipodomys* species (Ernest and Brown 2001a; Thibault et al. 2010a). Ernest and Brown (2001b) and Ernest et al. (2008) consider the Portal assemblage to exhibit compensatory (or zero-sum) dynamics, in which the same amount of energy is consumed but the species consuming the resources change. For example, over time, smaller rodents occupied the site with a concomitant drop in mean biomass but their numbers increased so as to consume similar amounts of resources (White et al. 2004). Such zero-sum dynamics are also indicated by the bird community study of Kaphengst and Ward (2008) reported on earlier in section 9.1.2.3 'Birds'.

In the desert of northern Chile, Meserve et al. (2011a) found that since about the year 2000 the small-mammal assemblage has started shifting from dominance by rapidly breeding, short-lived sigmodontine rodents, such as the olive grass mouse (*Abrothrix olivaceus*), the long-haired grass mouse (*Abrothrix longipilis*), Darwin's leaf-eared mouse (*Phyllotis darwini*), and the long-tailed rice rat (*Oligoryzomys longicaudatus*), and a single marsupial species, the elegant mouse opossum (*Thylamys elegans*), to dominance by slower reproducing, long-lived caviomorphs such as degus (*Octodon degus*) (Meserve et al. 1996). This shift could represent a response to more equitable rainfall between high-rainfall years and the lack of intervening droughts, a suggested consequence of global climate change in this region. Experimental removal of the dominant small mammal (the degu, *Octodon degus*) from the Chilean site (Kelt et al. 2015) revealed no evidence for energetic or functional compensation unlike the Portal study in North America; energy consumption remained significantly lower on degu exclusions relative to control plots after 17 years of exclusion. Kelt et al. (2015) emphasize that this lack of energetic or functional compensation occurred despite the similarity in the geographic species pools, so-called γ diversity (median number of species for South American sites was 21.5 vs 20 for North American sites). Kelt et al. (2015) also performed a macroecological assessment of energetically equivalent species at 394 arid sites in North America, the Gobi Desert, and South America and found that the number of potentially equivalent species was lower than (Gobi) or similar to (South America) that found in North America. However, when these authors segregated the species by trophic groups, these faunas differed markedly. As noted by Fox (2011), North American sites included large numbers of granivorous species whereas South American sites were dominated by omnivores. The more general trophic strategy in the South American sites would be expected to facilitate compensatory responses within local faunas, suggesting either that the Chilean site is anomalous or that other factors are governing local dynamics. Further studies of other desert assemblages need to be conducted before claims can be made about general patterns.

Dickman et al. (2011) have also studied small-mammal dynamics in spinifex grassland of central Australia. Southern hemisphere sites are subject to additional variation in rainfall due to the effects of El Niño-Southern Oscillation (ENSO), which causes long-term droughts and high rainfall. Although ENSO may affect North America too, its effects in South America are direct and strong. Australia is also particularly strongly impacted by ENSO, as is southern Africa (Lovegrove 2003). Dickman et al. (2011) were particularly interested in the effects on trappability of small mammals during periods of extreme and prolonged droughts. They predicted that these mammals may use woodlands as refugia during droughts. One species, the sandy inland mouse (*Pseudomys hermannsburgensis*), used woodland refugia as they had predicted. However, this species was still trapped in grasslands as well as woodlands during droughts. Both the spinifex hopping mouse (*Notomys alexis*) and brush-tailed mulgara (*Dasycercus blythi*) continued to use grassland more than woodland during drought and nondrought periods. They concluded that woodland patches contribute importantly to the persistence of *Pseudomys hermannsburgensis* during droughts, but capture success of *Notomys alexis* and *Dasycercus blythi*, which declined in density during extreme droughts, either used unidentified refugia or simply occurred at such low densities in grassland habitat that their chances of being captured were very small.

10 Human Impacts and Desertification

10.1 The sensitive desert ecosystem: myth or reality?

There is a common myth that deserts are extremely sensitive to perturbation. While it is true that tracks made decades ago can still be seen in certain desert areas (Belnap and Warren 2002; Kade and Warren 2002), there are also large regions of deserts that show little negative impact of heavy use by humans. This paradox can be explained by considering the interactions between the high spatial and temporal variability in rainfall and patterns of human disturbance.

Desertification is of great concern in many parts of the world, yet people struggle to define it. Historical patterns of climate indicate that there are cycles of drought and also cycles of higher rainfall, more so in arid lands where the coefficient of variation in rainfall is higher than in mesic environments (see Chapter 2; Nicholson 1978; Dettinger et al. 1998; Almeida et al. 2004). These cycles are often correlated with El Niño-Southern Oscillation (ENSO) cycles (Ropelewski and Halpert 1987; Dettinger et al. 1998) and, in Africa, with the Indian Ocean Dipole (IOD) (Williams and Hanan 2011). Williams and Hanan (2011) have also shown that there can be interesting oscillations between these two large-scale weather patterns with IOD causing increases in photosynthesis during ENSO's conventional decline in photosynthesis (associated with drought).

Giannini (2010) has considered the factors that cause desertification in the Sahel in West Africa. Giannini (2010) considers two mechanisms—one is anthropogenic warming (through land-use changes) that changes continental climate indirectly because warming of the oceans increases moist static energy at higher altitudes, affecting vertical stability globally from the high altitudes downwards, resulting in the drying of the Sahel. In the second mechanism, Giannini (2010) considers an increase in anthropogenic greenhouse gases that drives direct continental change with an increase in net terrestrial radiation at the surface that increases evaporation. Such increased evaporation favours vertical instability and near-surface convergence from the ground upwards. In both of these cases, the temperature of the ground surface increases but with the first mechanism precipitation and evaporation decrease while the second mechanism suggests an increase in evaporation and precipitation. Note that Giannini (2010) is mooting that it is anthropogenic causes in both mechanisms,

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regardless of the mechanism. Indeed, drought alone cannot be responsible for desertification but can add to the problem. Losses of agricultural productivity can often be associated with the process of desertification (Nyssen et al. 2009), although these can have other causes such as declining economic returns from certain agricultural products (i.e. not necessarily related to declines in agricultural productivity per se; Verstraete et al. 2009). Indeed, it is the long-term decline in productivity and ecosystem function that are most closely tied to desertification (Nyssen et al. 2009). These are usually caused by direct human intervention. However, Emanuel et al. (1985) have predicted a 17% increase in global desert lands because of climate changes expected with a doubling of atmospheric CO_2 concentrations, which may exacerbate the problem of desertification. The most important cause of desertification is pastoralism (Fig. 10.1), although many parts of the Middle East are most negatively affected by agricultural use (Bruins 2012; Pietsch and Mabit 2012). Among the negative impacts of desertification, soil salinization (Gutierrez and Johnson 2010; Ding and Yu 2014), harvesting of woody plants for fuel (including use by non-desert communities; Kaschula et al. 2005; Kaschula and Shackleton 2009), low agricultural productivity (especially in producing crops not ideally suited to the lands; Achten et al. 2013), and housing and related development (Sharma et al. 2013) are among the most obvious.

In South Africa, desirable forage species may be replaced by species that are inedible to livestock (Milton et al. 1994; Mbatha and Ward 2006), while in some parts of southern Africa, as well as in North America, the replacement of grasslands by woody species are particularly negative effects of desertification (Ward 2005a; Browning and Archer 2011). In South Africa, up to 20 million ha is affected by woody plant encroachment (Hoffman and Ashwell 2001; Ward 2005b; Ward et al. 2014). Desertification in some form is estimated to have occurred over about 42% of arid and semi-arid lands in Australia (Ludwig and Tongway 1995), with the interactions of agriculture, infrastructure extension, and increased aridity the main concerns (Geist and Lambin 2004). The most common form of desertification in Australia is loss of perennial grasses from

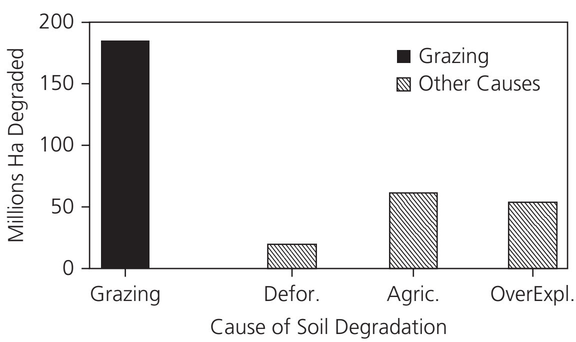

Fig. 10.1 Causes of soil degradation in Africa. Defor. = deforestation; Agric. = agricultural; Overexpl. = overexploitation from various sources.

Source: From UNEP (2006).

grasslands, savannas, and open woodlands, often with a replacement by inedible shrubs (Eldridge et al. 2011; Eldridge and Soliveres 2014). Changing climate and land-use changes, including pastoralism, have resulted in rapid vegetation shifts, which alter the rates and patterns of soil erosion in dryland systems (Ravi et al. 2010). With the predicted increase in aridity and an increase in the frequency of droughts in drylands around the world, there could be an increasing dominance of abiotic controls of land degradation, in particular hydrologic and aeolian soil erosion processes (Ravi et al. 2010; Fig. 10.2). Further, changes in climate may alter the relative importance of wind versus water erosion in dryland ecosystems. Desert dust, driven by wind, is a major contributor of tropospheric aerosols, which affect global climate, air quality, and hydrological–biogeochemical cycles (Ramanathan et al. 2001; Hui et al. 2008; Field et al. 2010). In the Atacama Desert (Peru), desertification results from the replacement of perennial grasses with unpalatable native and exotic annuals and by an unpalatable tree *Acacia caven* (Fabaceae) (Ovalle et al. 1993). In the Monte Desert of Argentina, a woody tree *Geoffroea decorticans* (Fabaceae) invades the arid and semi-arid regions (Whitford 2002). In the Gobi and Taklamakan deserts of China, widespread dune formation has reduced agricultural productivity (Yang et al. 2005; see Fig. 10.3) and lowered water-table depths due to excessive water extraction (Zheng et al. 2006). Increased soil salinization has been caused by poor agricultural practices (Ma et al. 2005).

A number of examples of desertification can help understand the diversity of processes that may lead to desertification:

1. Sinclair and Fryxell (1985) have considered the Sahel as a classical disaster zone. This area on the southern edge of the Sahara has a huge human and livestock population. Sinclair and Fryxell (1985) consider the following scenario as being integral to understanding the problem (Fig. 10.4): when herds of animals are kept in fixed places they tend to overgraze. This leads to raised albedo levels, which in

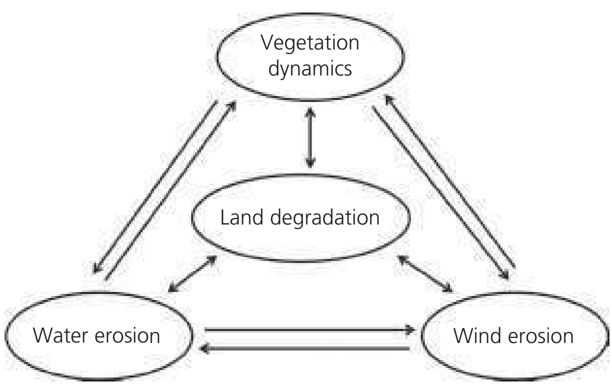

Fig. 10.2 Conceptual diagram showing the stages of grassland degradation in the Chihuahuan Desert along with changes in functional connectivity, soil erosion rates, and biodiversity.
Source: From Ravi et al. (2010). With kind permission of Elsevier.

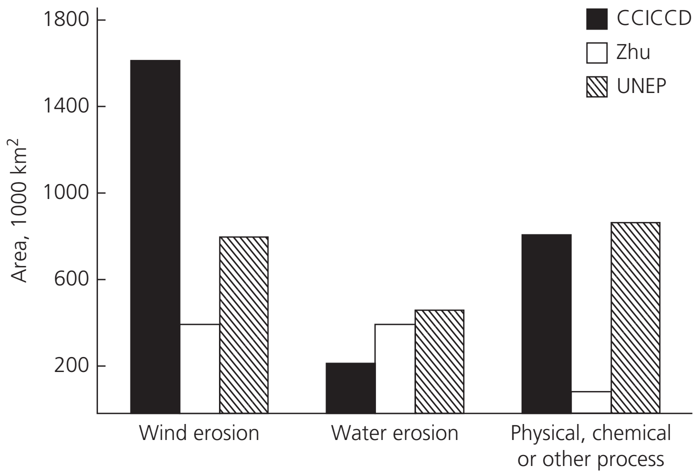

Fig. 10.3 Main causes of desertification in China, showing differences among estimates made by three sets of authors.

Source: From Yang et al. (2005). With kind permission of Elsevier.

turn leads to hotter soil, which in turn leads to reduced thermals and less rain. The situation perpetuates itself because less rain means that the livestock are forced to eat the remaining vegetation. On the other hand, if livestock are allowed to be nomadic, albedo levels are ultimately lower, which increases rainfall (Fig. 10.4). This is consistent with Hardin's (1968) *tragedy of the commons* model, which holds that in a communal system, each person stands to benefit by one animal for each one owned but the costs are shared by all, leading to the ultimate degradation of the lands. Schlesinger et al. (1990) have followed on from Sinclair and Fryxell's model to include more explicit incorporation of the positive feedback effects of moisture and the vegetation to include nutrients, especially nitrogen, which is the

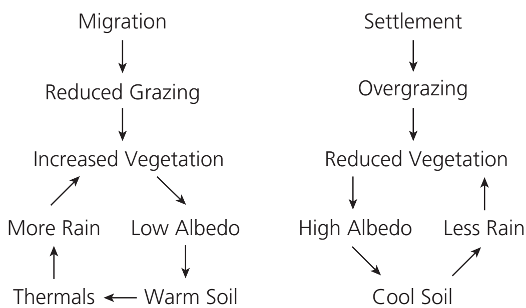

Fig. 10.4 Sinclair and Fryxell (1985) consider the absence of nomadism (migration) as being integral to understanding the problem of rangeland degradation.

Source: From Sinclair and Fryxell (1985). With kind permission of National Research Council, Canada.

single most important limiting nutrient in deserts (Fig. 10.5). Schlesinger et al. (1990) consider the effects of increasing soil heterogeneity to be among the most important negative effects on arid regions, and one that can lead to the conversion of grasslands into shrublands (Schlesinger et al. 1996; see section 10.2.2, 'Woody plant encroachment'). Greater soil heterogeneity can also be caused by off-road motor vehicles, which leads to the channelization of run-off and increased soil erosion (Webb 1982; Webb et al. 2009).

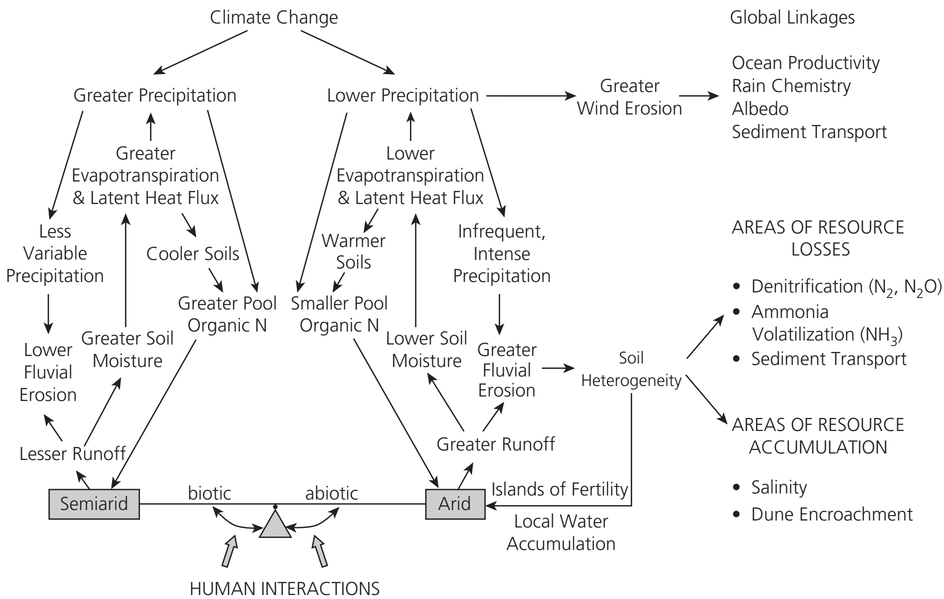

Fig. 10.5 The main effects of desertification on nutrients in arid ecosystems.

Source: From Schlesinger et al. (1990). With kind permission of the American Association for the Advancement of Science.

2. Erosion in Negev Desert (Israel) wadis has been continuing since climatic changes during the Late Pleistocene–Early Holocene period, resulting in declines in dust deposition (Ward et al. 2001; Avni et al. 2006). Severe erosion causes the formation of gullies and channels, resulting in the formation of waterfalls during the winter floods in many wadi systems in the central Negev Desert of Israel. These were caused by higher rain intensity at the end of the Pleistocene (Avni et al. 2006). In some areas, erosion of the original loess substrate has been complete, so that the underlying rock has been exposed. Establishment of run-off harvesting farms in the third century CE (mostly by Nabatean people) interrupted the Holocene natural erosion and gully incision, and led to the redeposition of up to 3.5 m of fine alluvial loess sediments originating from Late Pleistocene loess sections (Bruins 2012) as run-off from the hillslopes accumulated in the wadis. Ward et al. (2001) examined the effects of this erosion in four wadis in the central

Negev Desert on soil nutrients and plant community structure. They found significant negative effects of erosion on soil organic carbon, nitrate nitrogen, and water-holding capacity. Erosion resulted in an increase in plant species richness and significantly altered plant community structure in eroded areas of wadis. In addition to the loss of biodiversity that may result, this erosion may result in economic hardship for the Bedouin peoples whose herds depend on these resources (Ward et al. 2001). The establishment of run-off harvesting agriculture, which resulted in the accumulation of re-deposited loess sediments from hillslopes, counteracted the natural trend of soil erosion (Avni et al. 2006).

In Inner Mongolia, Avni et al. (2010) found that gullies have been a long-term geomorphic feature at the margins of the Gobi Desert since at least the Middle Pleistocene. During the Holocene, the erosion of the Pleistocene loess on the hills led to the burial of the valley floors by the redeposited sediments at a rate that decreased from 3.2 m ka^{-1} near the hills to 1–0.4 m ka^{-1} in the central part of the river forming the Chifeng Valley, in Inner Mongolia (Fig. 10.6). This

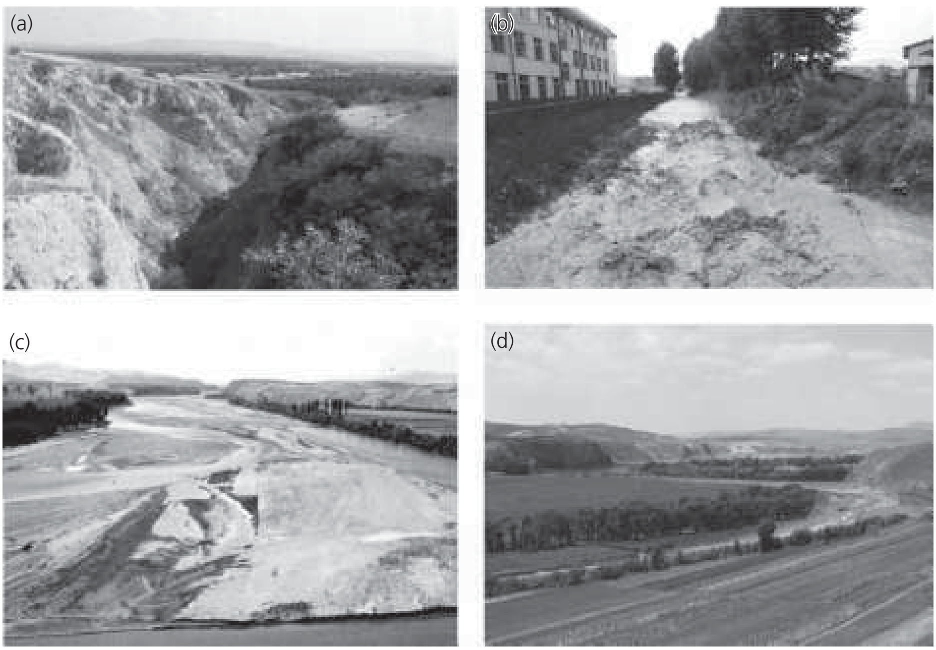

Fig. 10.6 General view of the valleys south of the city of Chifeng: (a) Wide valleys surrounded by hills, covered with thick loess sediments. Deep gullies contribute their eroded sediments to the valleys downstream. (b) A flash flood resulting from heavy summer rains, heavily loaded with eroded loess sediments, endangers present infrastructure and buildings in Chifeng Valley. (c) Shallow rivers, frequently overflowing, occupying the bottom of the valleys. Note the present high sediment load causing aggradation along the valley floor. (d) The present river meanders throughout the entire valley floor.

Source: From Avni et al. (2010). Kind permission of John Wiley and Sons.

rapid accumulation and the frequent shifts of the courses of the river prevented the construction of permanent settlements in the valley floors, a situation that changed due to man-made control of the local rivers from the tenth century AD (Avni et al. 2010).

3. Ward and Rohner (1997) studied the causes of large-scale mortality of *Acacia* trees in Negev Desert wadis. In 75 wadis distributed across the Negev Desert, they found that low-lying bridges were the cause of this problem. These bridges, pejoratively called 'Irish bridges' by the British soldiers during the Mandate period (1917–48) because they pass under rather than over the ephemeral waters, do not allow water to pass as easily to the lower parts of the rivers. Consequently, mortality of Acacias is far higher (as high as 61%) on the lower side of these bridges than on the upper side (Fig. 10.7).
4. High soil salinity occurs naturally in the desert environment (Crawford and Gosz 1982). However, soil salinization is associated with irrigated areas that have poor water management, raising the natural salinity of the soil to the soil surface (Cui and Shao 2005). Another way in which arid areas can have raised levels of soil salinization occurs when native vegetation is removed, which alters water balance and evaporative flux (Amezketa 2006). Although climate, natural drainage patterns, topographic features, geological structure, parent material, and distance to the sea are natural factors influencing soil salinity, inappropriate irrigation methods, poor water quality, insufficient drainage, poor land management, overexploitation of groundwater, the clearing of trees, and the alteration of the natural water balance are important anthropogenic (agricultural) factors (Tang and Zhang 2001; Cui and Shao 2005; Amezketa 2006; Masoud and Koike 2006).

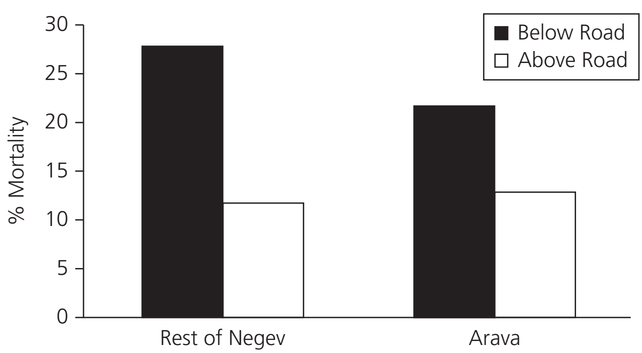

Fig. 10.7 Acacia *raddiana* mortality on the lower side of low-lying bridges is far higher than on the upper side. Similar values were recorded in the Syrian-African Rift valley (Arava) and in the rest of the Negev.

Source: Modified from Ward and Rohner (1997). With kind permission of Springer.

Fig. 10.8 Agriculture along the Arava (Syrian-African Rift Valley) in the Negev Desert of Israel.
Source: Photo courtesy of Doron Nissim.

Soil salinization reduces soil quality, limits the growth of crops, constrains agricultural productivity, and in severe cases, leads to the abandonment of agricultural soils (Amezketa 2006) (Fig. 10.8). Thus, it is in desert margins that this type of desertification is most likely to occur. In China, about half of the land area receives less than 200 mm year^{-1} of precipitation (Tang and Zhang 2001). Soil salinization in northwestern China affects about 2 million ha, which makes up about one-third of the saline area of China (Cui and Shao 2005). In the northwestern desert of Egypt (part of the Sahara), according to Misak et al. (1997), the rate of the rise in the groundwater table in the Siwa Oasis was 1.33 cm year^{-1} from 1962 to 1977, while during 1977–90 it was 4.6 cm year^{-1}. Masoud and Koike (2006) found that soil salinization led to vegetation death in the Siwa Oasis after the year 2000 largely as a result of improper soil drainage and a lack of an effective water resource management system. The water table has now reached the ground surface in some areas, causing an advanced stage of salinization. As a result, extensive patches have been gradually converted into salt marshes (Masoud and Koike 2006).

10.2 Pastoralism is the most important use of desert lands

The most important cause of desertification is grazing by livestock (Milton et al. 1994; UNEP 1996; Middleton and Thomas 1997) (Fig. 10.1). In general, where nomadic pastoralism can continue, these effects are less pronounced or even absent (Sinclair and Fryxell 1985). Similarly, where plants have sufficient time to recover from heavy grazing, these effects can be minimized. Some of the most obvious negative consequences of heavy grazing include the following:

1. *Piosphere effects:* Osborn et al. (1932) were the first in Australia to recognize the radial symmetry in grazing intensity that develops around a water point. Osborn et al. (1932) used this radial symmetry to examine the effects of grazing on vegetation along transects radiating from water. Grazing impact is greatest close to a water point and decreases with distance from the water because livestock have to return regularly to drink. Lange (1969) coined the term *piosphere* for this water-focused grazing pattern. Valentine (1947) also drew attention to the graduated use of forage away from an artificial water point in a black grama (*Bouteloua eriopoda*) grassland in the Chihuahuan Desert of North America. Valentine (1947) proposed that overstocking of lands in the southwestern desert areas of the United States had caused the failure to account for non-uniform use of forage in a paddock. As well as grazing effects, there are also effects from trampling and dust associated with the movement of animals close to the water point (Andrew and Lange 1986a, b). James et al. (1999) have described the piosphere effects in arid Australian ecosystems as follows:

    a. The area near a watering point is usually bare, but supports short-lived, often unpalatable, trample-resistant species after rain. Trampling is most obvious within 100 m of the water point. This zone is often called the 'sacrifice zone'.
    b. A dense zone of unpalatable woody shrubs usually occurs immediately beyond the denuded area.
    c. Palatable perennial plants decline in both abundance and species richness within zones a and b.
    d. Species richness does not change consistently with increasing distance from water points.

An important effect can be seen in fenceline contrasts (e.g. Figs. 10.9a and b). Here, too, differences can be observed for the wrong reason because they may merely indicate short-term differences caused by grazing a paddock immediately prior to that observation. Nonetheless, Hendricks et al. (2005) in arid Namaqualand, South Africa, and Smet and Ward (2005, 2006) in the arid Northern Cape, South Africa, have shown that piosphere effects around water points can be significant. Similar techniques were used by Hanan et al. (1991) to examine piosphere effects around boreholes in Senegal, in the Sahel region of Africa. However, Hanan et al. (1991) found no consistent patterns in primary production with increasing distance from water points during the wet season and concluded that piosphere effects on vegetation, if present, were overridden by variation due to local topography, soil, and rainfall patterns. Jeltsch et al. (1997) measured differences in vegetation at two sites in the Kalahari Desert (South Africa/Botswana). They then mathematically simulated a high rainfall site (385 mm) and a low rainfall site (220 mm). Jeltsch et al. (1997) have shown that distinct piospheres occur at the high rainfall site (as indicated by James et al. 1999 mentioned earlier), whereas at the low rainfall site, piosphere zone development is limited and influenced by rainfall alone.

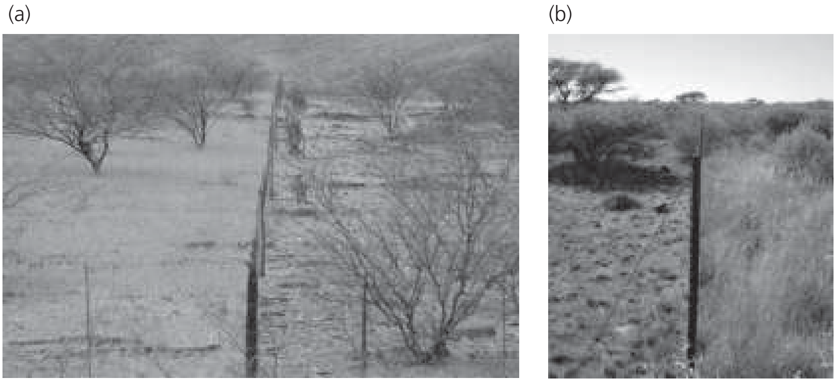

Fig. 10.9 Fenceline contrast from (a) the Namib, Namibia (mean annual rainfall (MAR) = 150 mm), and (b) from the arid Northern Cape province, South Africa (MAR = 360 mm).

2. *Communal ranching*: Ward et al. (2000b) recorded that the communal ranching area of Otjimbingwe in Namibia (mean annual rainfall = 165 mm) had experienced a change in the people occupying these lands. During the time that Charles John Andersson (1856) occupied the lands as a trader, all of the people living there were otjiHerero speakers. The Damara peoples lived at least 60 km away (Fig. 10.10). The Herero people are very closely associated with their cattle, relying on them for meat and milk. In contrast, the Damara people were mostly

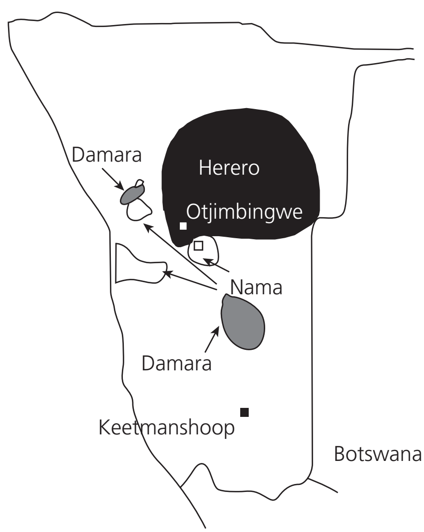

Fig. 10.10 Map of distribution of tribal groups of people around Otjimbingwe. The main tribal groups in this region are Herero, Damara, and Nama.

vegetarian, although some of them consumed small stock such as goats and sheep. Today, there are approximately the same number of Herero and Damara people living in Otjimbingwe. This led Ward et al. (1998, 2000b) to believe that a possible reason for the change in population occupying Otjimbingwe had been land degradation, especially since Andersson (1856) and Lau (1989—from Andersson's diaries) had recorded as many as 14,000 cattle being present at certain water points in Otjimbingwe during Andersson's time there. Ward et al. (2000b) found that the numbers of people had increased dramatically since the mid-1950s. Fuller (1993) found that the number of people living in Otjimbingwe fluctuated considerably between 1920 and 1955, but that there were now some 8,500 people living there (Fig. 10.11). In addition, people had been able to produce as much as 95 tons of wheat in the Swakop River that runs ephemerally through Otjimbingwe.

Ward et al. (1998) compared the diversity of plants in the communal area of Otjimbingwe that has been heavily grazed for at least 150 years with that of several surrounding commercial cattle and sheep ranches where mean stocking density was about 10 times lower. No significant difference in diversity, plant species richness, or soil quality was found. However, within the 117,000-ha communal ranch, vegetation around water points that had been in use for 150 years (i.e. these were sites mentioned as having large stock numbers by Andersson (Lau 1989)) was more degraded than vegetation near water points that had only been in use for about 10 years (Fig. 10.12) (see item 1 in this list, 'Piosphere effects'). This indicates that herbivores can have strong negative impacts on vegetation of deserts but that such impacts may take a very long time (at least 80 years in this case) to manifest themselves. Ward et al. (1998) also found that there were differences in the diversity of large mammals between communal and

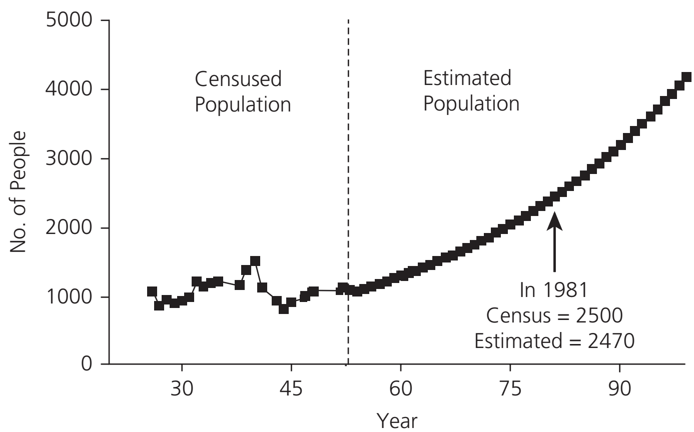

Fig. 10.11 Fuller (1993) found that the number of people living in Otjimbingwe fluctuated considerably between 1920 and 1955. There are currently (2008) some 8,500 people living there. A 3% increment in population growth (Namibia's national average population growth rate) was used post-1955 to predict population growth. Note the similarity in values between the last population census and the predicted value.

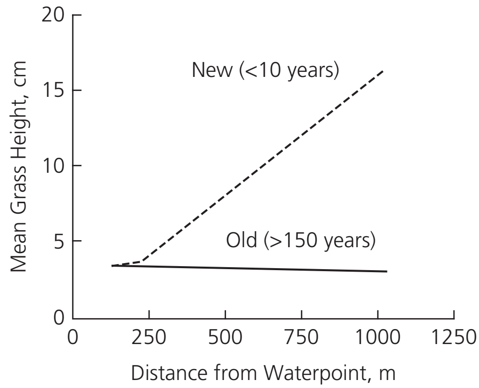

Fig. 10.12 Vegetation around water points that had been in use for 150 years (i.e. these were sites mentioned as having large stock numbers by Charles John Andersson) was more degraded than vegetation near water points that had only been in use for about 10 years. Lines are regression lines of sample means.

commercial ranches. Commercial ranches had a variety of species such as kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazelle*), Hartmann's mountain zebra (*Equus zebra hartmannae*), and springbok (*Antidorcas marsupialis*), while the only species that the communal ranch had was the steenbok (*Raphicerus campestris*). Fuller (1993) found that up to 95 tons of wheat were produced in the ephemeral Swakop River. However, this no longer occurs because two reservoirs were built upstream to provide water to the capital city of Windhoek and to Okahandja (see water flow in the Swakop River; Fig. 10.13), causing water to flow through Otjimbingwe only a few times since the dams were built in the mid-1970s.

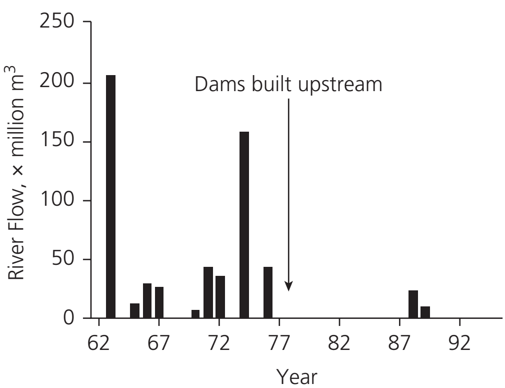

Fig. 10.13 Water flow in the Swakop River at Westfalenhof Weir immediately upstream from Otjimbingwe. Water flowed through Otjimbingwe only a few times since the reservoirs were built in the mid-1970s to provide water to the capital city of Windhoek and to Okahandja, resulting in an absence of wheat production in the ephemeral Swakop River at Otjimbingwe.

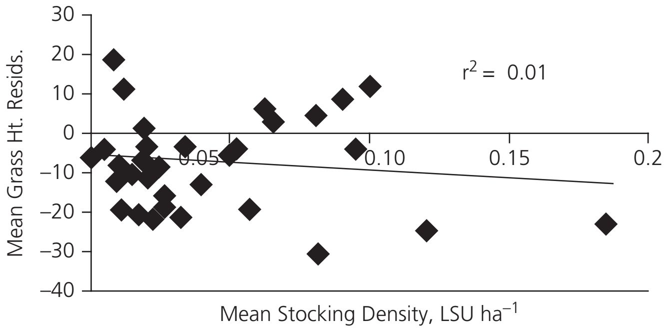

Fig. 10.14 There was no correlation between the residuals of grass production (regressed against mean annual rainfall to account for variation along the rainfall gradient) and stocking density (expressed as large stock units (LSU) per hectare) either in the current season or when averaged over the previous 11 years, as indicated in the figure.

Source: From Ward and Ngairorue (2000). With kind permission of Elsevier.

3. *Grazing along a rainfall gradient*: In a large-scale study in Namibia at 31 sites along a rainfall gradient from 100 to 450 mm per annum, there was no correlation between the residuals of grass production (regressed against mean annual rainfall) and stocking density either in the current season or when averaged over the previous 11 years (Ward and Ngairorue 2000; Fig. 10.14). However, when they compared data along the same gradient between 1939 and 1997, grass production in 1997 was approximately 50% lower than in the earlier period (Ward and Ngairorue 2000) (Fig. 10.15). This is yet another example of the longer-term impact of herbivory in such systems.

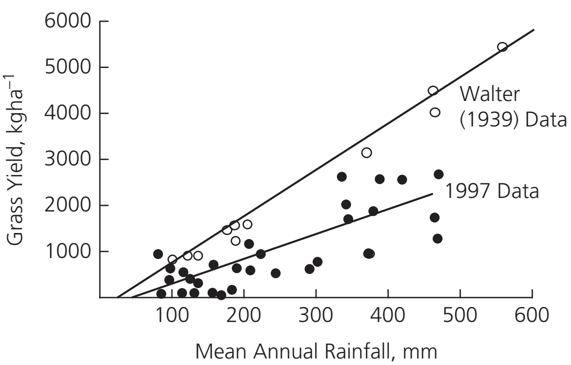

Fig. 10.15 Ward and Ngairorue (2000) compared data along the same gradient between 1939 and 1997; grass production in 1997 was approximately 50% lower than that in the earlier period.

Source: From Ward and Ngairorue (2000). With kind permission of Elsevier.

10.2.1 Oscillations of vegetation and herbivore populations

Researchers have become increasingly aware in recent years that arid grazing ecosystems are non-equilibrial, event-driven systems (Westoby 1980; O'Connor 1985; Milchunas et al. 1988, 1989; Venter et al. 1989; Westoby et al. 1989; Hoffman and Cowling 1990; Gillson and Hoffman 2007). Ellis and Swift (1988) contended that rainfall in arid regions is the major driving factor and has the ability to 'recharge' a system that suffers heavy grazing pressure. This can lead to oscillations of herbivore and plant populations, as envisaged for the arid Turkana region of Kenya by Ellis and Swift (1988) (Fig. 10.16).

Indeed, it has been claimed that where pastoralists are able to maintain their activities on a large spatial scale by migrating to areas where key rich resources can be exploited, allowing previously used resources time to recover, negative density-dependent effects of grazing on plant biodiversity do not develop (Sinclair and Fryxell 1985; Ellis and Swift 1988; Behnke and Abel 1996). Illius and O'Connor (2000) have suggested that herbivore populations use key preferred habitats or resources for much of the year and only move out of those habitats when resources are limiting. Consequently, one might not find any significant effects of mammalian herbivory in arid ecosystems at large, yet negative density-dependent effects of heavy grazing are likely to be found in key habitats. Where these habitats are provided with artificial water points, such problems might be particularly acute. Based on the field data from a Kalahari Desert grazing system, spatially explicit modelling by Weber et al. (2000) indicated that the existence of long-term negative effects of herbivory depends on whether herbivores cause reductions in plant productivity (rather than short-term reductions in plant biomass) and local mortality of plant species during periods of reduced plant availability (see also O'Connor 1991). Such mortality may result in a change in plant species composition, and if the newly dominant species are less

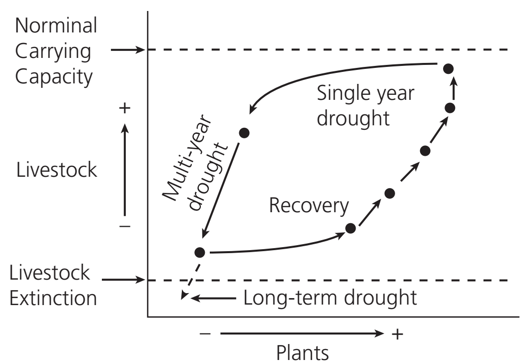

Fig. 10.16 Oscillations of herbivore and plant populations as envisaged for the arid Turkana region of Kenya.

Source: From Ellis and Swift (1988). With kind permission of Society for Range Management.

palatable to herbivores, then it will ultimately lead to rangeland degradation. Thus, Ellis and Swift's (1988) model mentioned earlier may be suitable for arid vegetation only if grazing does not differentially affect species and thereby alter species composition through changes in competitive interactions. Should there be any changes caused by, for example, changes in competitive interactions or grazing-induced changes in dominance of particular species, the Ellis and Swift (1988) model will be inappropriate.

10.2.2 Woody plant encroachment

One of the most interesting, and enigmatic, purported effects of herbivory by large mammals is the initiation of woody plant encroachment (in North America, this phenomenon is known as shrub encroachment and in southern Africa it is called bush encroachment). In the past 50 years, evidence has accumulated suggesting that arid and semi-arid ecosystems throughout the world are being altered by woody plant encroachment (Hennessy et al. 1983; Idso 1992; reviewed by Archer et al. 1995; Scholes and Archer 1997). Woody plant encroachment is the suppression of palatable grasses and herbs by encroaching woody species (Figs. 10.17a and b). These woody species are often unpalatable to domestic livestock because they are thorny or have high fibre content (Lamprey 1983; Scholes and Walker 1993; Ward 2005b).

Factors causing bush encroachment are poorly understood. The first attempt at a general explanation for bush encroachment was Walter's (1939) two-layer hypothesis for tree–grass coexistence (Walter 1954; Noy-Meir 1982). Walter (1939, 1971) explained the coexistence of these two different life forms in terms of root separation. He assumed water to be the major limiting factor for both grassy and woody

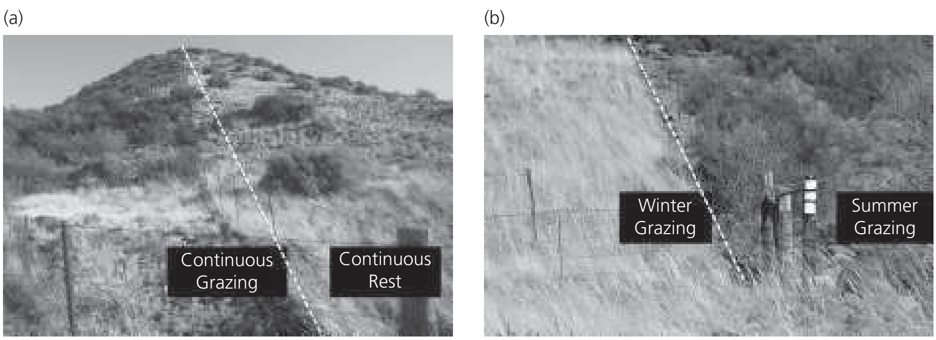

Fig. 10.17 Woody plant encroachment at Middelburg, Eastern Cape caused by grazing. Mean annual rainfall is 300 mm. There were two sheep per acre, which is the recommended stocking rate for this region. (a) Comparison of continuous grazing versus continuous rest, and (b) comparison of summer grazing versus winter grazing. The summer grazing leads to encroachment in this summer-rainfall area, presumably because the grasses are still growing at this time. There are four encroaching species in these plots: *Searsia erosa, Searsia burchellii, Diospyros lycioides*, and *Eriocephalus ericoides*.

plants and hypothesized that grasses use only topsoil moisture, while woody plants mostly use subsoil moisture. Under this assumption, removal of grasses (e.g. by heavy grazing) allows more water to percolate into the subsoil, where it is available for woody plant growth. This allows for mass recruitment of trees, leading to bush encroachment. Note that in arid and semi-arid ecosystems, cohorts of similarly aged trees have been widely reported, indicating repeated phases of mass recruitment (Reid and Ellis 1995; Wiegand et al. 2005, 2006). Hence, it is the initiation of bush encroachment that is considered the crucial stage in arid ecosystems and not the control of adult tree densities as may be the case in mesic regions (Higgins et al. 2000).

10.2.3 Invasive species

The most reliable indicator of potential for a plant species to invade is weedy or invasive behaviour, such as taking over disturbed habitats, by that species or by congenerics (Scott and Panetta 1993). Repeated introductions over many years may further increase the probability that a species will become invasive (Scott and Panetta 1993). Plant invasions in Australian, North American, and the Karoo of South Africa habitats have been most severe along watercourses (Loope et al. 1988; Milton et al. 1999; Cronk and Fuller 2001). For example, invasions by *Tamarix* from Asia have followed the arid portions of the Colorado River and the Rio Grande in North America, and the Finke River in Australia. In the Karoo, the extent of invasion by exotic *Tamarix* species may be underestimated because they morphologically resemble a native species, *Tamarix usneoides* (Milton et al. 1999). All *Tamarix* trees are reputed to increase soil salinity, to lower water tables, and to reduce diversity of reptiles and birds (Griffin et al. 1989; Ellis 1995; Milton et al. 1999). *Nicotiana glauca* has invaded rivers in North America, Australia, and the Middle East (Milton et al. 1999; pers. obs.).

Milton et al. (1999) considers four families of plants in the arid Karoo (South Africa) to be particularly invasive, namely, Cactaceae (especially *Opuntia*), Fabaceae (especially *Prosopis*), Chenopodiaceae (especially *Atriplex* and *Salsola*), and Poaceae (especially perennial African C_4 species and annual C_3 species). *Opuntia ficus-indica* has been a major pest in the Karoo and *Opuntia stricta* and *Opuntia inermis* in Australian habitats. Feral livestock, especially pigs and donkeys, took refuge in these Australian Desert areas and their control is very difficult. Severe grazing took place in these areas. In the Karoo, Du Toit (1942) estimated that *Opuntia ficus-indica* infested as much as 900,000 ha (see also Brutsch and Zimmermann 1993). A phycitid moth (*Cactoblastis cactorum*) was introduced from Australia in 1932 (it originally came from South America; Frawley 2014) and a cochineal bug (*Dactylopius opuntiae*) was brought in and proved to be effective biological control agents against *Opuntia ficus-indica.* The South American *Cactoblastis cactorum* moth had proved to be an effective form of biological control for prickly pear, *Opuntia* and *Nopalea* spp. in Australia, beginning in 1926 (Frawley 2014). *Dactylopius opuntiae* was found to be more effective in South Africa (Milton et al. 1999). Interestingly, *Opuntia ficus-indica* occurs in semi-arid areas of the Middle East but does not invade beyond the livestock maintenance areas (pers. obs.). The African lovegrasses, *Eragrostis curvula* and *Eragrostis lehmanniana*, were introduced from Africa into North American deserts in the 1930s in an attempt to reclaim natural grasslands damaged by heavy grazing and cultivation (Bock et al. 1986, 2007) and are now spreading into undisturbed rangelands (McClaran and Anable 1992). Mediterranean annual grasses, particularly cheatgrass (*Bromus tectorum*), also invaded North American arid lands (Mack 1981). Milton et al. (1999) are concerned about the invasion of C_3 grasses into the Succulent Karoo, which is widely regarded as the most species-rich succulent flora.

10.2.4 Global climate changes

Global climate changes are predicted for many arid regions. For example, climate change is predicted to alter the rainfall regime in the Eastern Mediterranean Basin: total annual rainfall will decrease, while seasonal and interannual variation in rainfall will increase. Such changes in the rainfall regime could potentially lead to large-scale changes in aboveground net primary productivity (ANPP) in the region. Golodets et al. (2013) conducted a study of herbaceous ANPP along an entire regional rainfall gradient, from desert (90 mm mean annual rainfall (MAR)) to Mesic-Mediterranean (780 mm MAR) ecosystems (Fig. 10.18), using the largest database ever collated for herbaceous ANPP in Israel. Their aim was to predict consequences of climate change for rangeland productivity. They found that herbaceous ANPP increased with increasing rainfall along the gradient, but there was strong dependence on rainfall within dry sites only. Golodets et al. (2013) consider that climate change is more likely to affect herbaceous ANPP of rangelands in the arid end of the rainfall gradient, requiring adaptation of rangeland management, while ANPP of rangelands in more mesic ecosystems is less responsive to variation in rainfall. I note that Golodets et al. (2013) were assessing the response of herbaceous ANPP only—changes to woody plant densities may have serious negative consequences for ANPP in many ecosystems (e.g. Baez and Collins 2008; D'Odorico et al. 2010; Ward et al. 2013), albeit not in the Negev or Judean Desert studied by Golodets et al. (2013).

In other studies conducted in the American Southwest, using rainfall manipulations and drought experiments, the results differed somewhat from those described by Golodets et al. (2013). For example, Baez et al. (2013) studied the effects of four years of rainfall manipulation and five years of artificial drought in a northern Chihuahuan Desert grassland. They found that drought consistently decreased the cover of the dominant C_4 grass, *Bouteloua eriopoda*, while rainfall addition caused a slight increase in cover. Contrastingly, the dominant C_3 shrub, *Larrea tridentata*, showed no response to either drought or rainfall addition. The cover of subdominant shrubs, grasses, and forbs responded far more to interannual variations in natural rainfall than either the drought or rainfall manipulations. They consider that the declines in grass production and resistance of shrub cover to alterations in drought indicate that droughts may be a serious factor leading to shrub invasion. This is in contrast to the data provided by Kraaij and Ward (2006), who showed in arid South Africa that rainfall addition (not drought) was a major cause of shrub invasion. In another study conducted in the U.S. Southwest, Collins et al. (2010) manipulated nocturnal

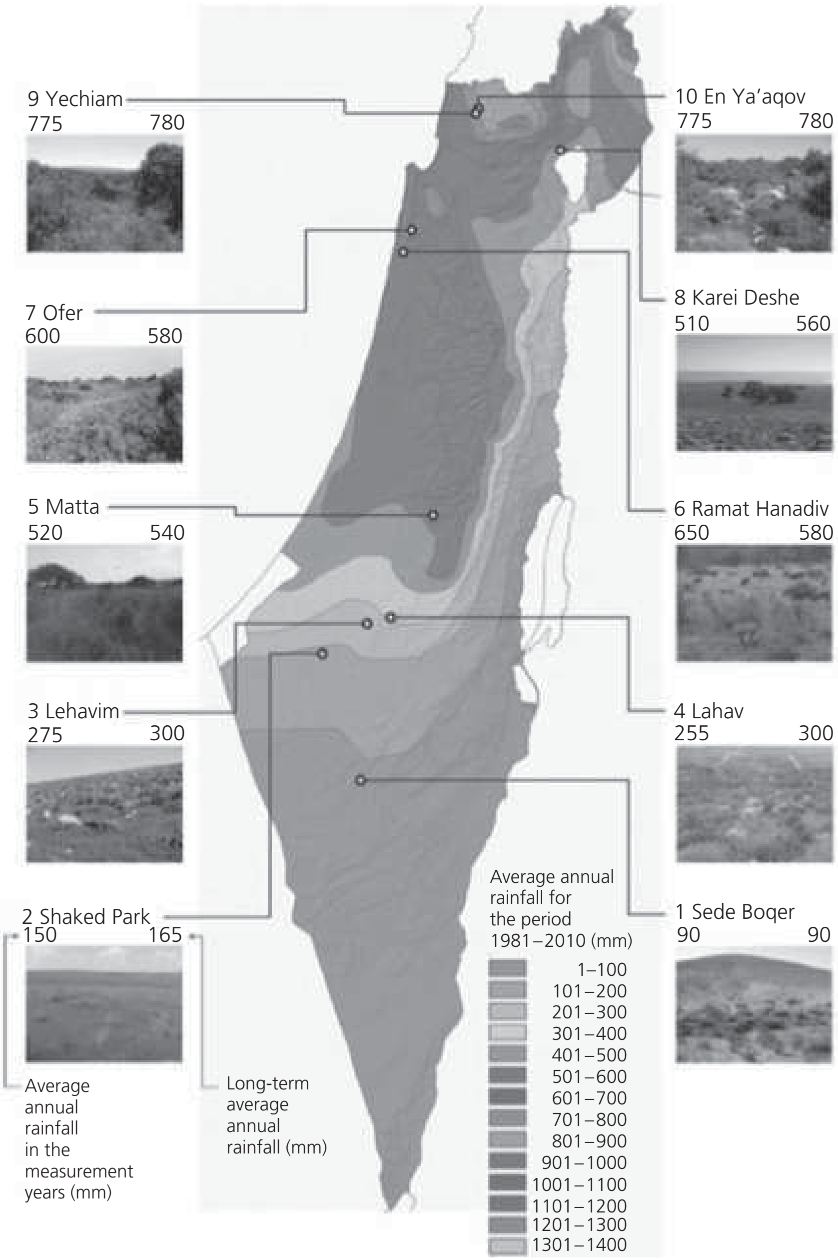

Fig. 10.18 Location of the ten research sites on the rainfall map of Israel and the Israeli-occupied territories, with typical landscape photographs. The map represents long-term mean annual rainfall for the period 1981–2010.

Source: From Golodets et al. (2013). With kind permission of Springer.

temperatures and nitrogen fertilization. After a single monsoon season, they found that warming significantly increased total plant cover but the responses among dominant species varied. Warming significantly increased cover of the C_4 grass *Bouteloua eriopoda* and caused a marginal increase in cover of the C_3 shrub *Gutierrezia sarothrae*. Nitrogen addition significantly increased the cover of *Bouteloua gracilis*. Their results (Fig. 10.19) showed that rapid responses in arid plant communities can occur (even over a single season) in response to nighttime warming and, occasionally, nitrogen fertilization.

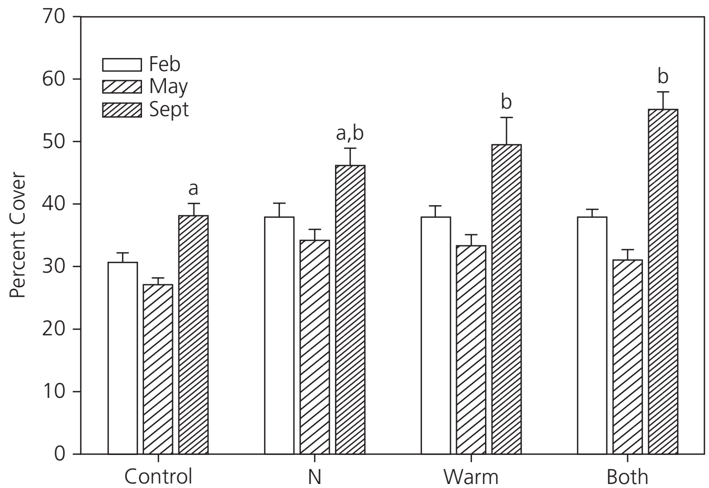

Fig. 10.19 Rapid responses in vegetation cover in the Chihuahuan Desert arid plant communities can occur (even over a single season: 2006) in response to nighttime warming and, occasionally, nitrogen fertilization.

Source: From Collins et al. (2010). With kind permission of Elsevier.

As indicated earlier, Emanuel et al. (1985) have predicted a dramatic increase in the global desert lands due to climate changes expected with a doubling of the atmospheric CO_2 concentrations, which may exacerbate the problem of desertification. Midgley and Thuiller (2007) have shown that some key Succulent Karoo plant lineages originated during cool Pleistocene times (Klak et al. 2004). Projected air temperatures under anthropogenic climate change are likely to exceed these temperatures significantly. Projected rainfall patterns are less certain, and projected values for coastal fog are unavailable, but if either of these two parameters also changes together with rising temperatures, this seems certain to threaten the persistence of, at least, narrowly endemic plant species (see projected changes in the distribution of such narrowly endemic Namaqualand (South Africa) shrub species as *Ruschia caroli* and *Ruschia robusta*; Fig. 10.20).

Unlike the predicted situation with rising temperatures and/or changes in rainfall and coastal fog, bush or shrub encroachment may become particularly acute in many

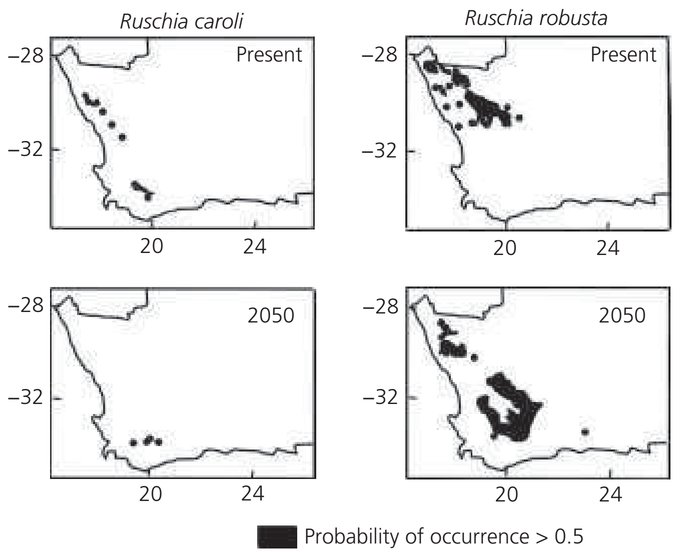

Fig. 10.20 Map of projected distributions of *Ruschia caroli* and *Ruschia robusta* in Namaqualand under projected global climate change.

Source: From Midgley and Thuiller (2007). With kind permission of Elsevier.

semi-arid habitats because of the effects of elevated CO_2. The net photosynthetic rates of C_3 plants relative to C_4 plants is likely to switch, so that higher photosynthetic rates will be recorded from C_3 plants such as encroaching shrubs rather than the current situation where C_4 grasses have higher photosynthetic rates. Consequently, C_3 shrubs are likely to grow faster under higher expected levels of CO_2 than grasses. If this is also associated with higher defence levels if these shrubs use tannins or other carbon-based polyphenols, then this problem will be exacerbated (Ward 2010).

It is often thought that there may be an increase in the amount of carbon stored in ecosystems where encroachment of woody vegetation has occurred because individual trees are usually much heavier than the grasses they have replaced. For this reason, shrub or bush expansion could be considered to have a positive effect on carbon stores or sinks. This may be viewed as positive by researchers studying climate change effects because carbon storage benefits ecosystems by reducing the effects of CO_2 emissions from fossil fuels into the atmosphere (Pacala et al. 2001; Guo and Gifford 2002). Jackson et al. (2002) studied woody plant invasion along a precipitation gradient from 200 to 1,100 mm year^{-1} by comparing carbon and nitrogen budgets and soil δ^{13} C profiles between six pairs of adjacent grasslands in the Chihuahuan Desert (North America) in which one of each pair of grasslands was invaded by woody vegetation 30–100 years ago. They found that there was a negative correlation between changes in soil organic carbon (and nitrogen) content and precipitation, with drier sites gaining and wetter sites losing organic carbon and nitrogen (Jackson et al. 2002) (Figs. 10.21a and b). They concluded that assessments based on increased carbon storage from woody plant invasions to balance emissions were incorrect. However, more recently, Barger et al. (2011) have found that, with more data added, this correlation with mean annual rainfall disappears. However, Barger et al. (2011) found that there were significant correlations with key soil parameters, specifically with soil bulk density and clay content. Soil bulk density (dry mass per unit volume) is a crucial soil property that influences infiltration rates, aeration, root proliferation, and plant growth. Sandy soils have high bulk density because they have larger pores but fewer of them. Fine silts and clays have low bulk density because they have more pores. Barger et al. (2011) found that there was a negative correlation between carbon and soil bulk density. They also found that there was a significant positive correlation with clay content because more organic carbon bound to clay colloids. Thus, bulk density and clay content are not truly independent because clays bind organic carbon and clays have low bulk density. Nonetheless, Barger et al. (2011) found that soils, rather than rainfall, were important for carbon sequestration. I note that Mureva et al. (submitted) have found a significant negative correlation with mean annual rainfall and no correlations with soil parameters, supporting the findings of Jackson et al. (2002) and *contra* Barger et al. (2011) in arid to humid South African soils.

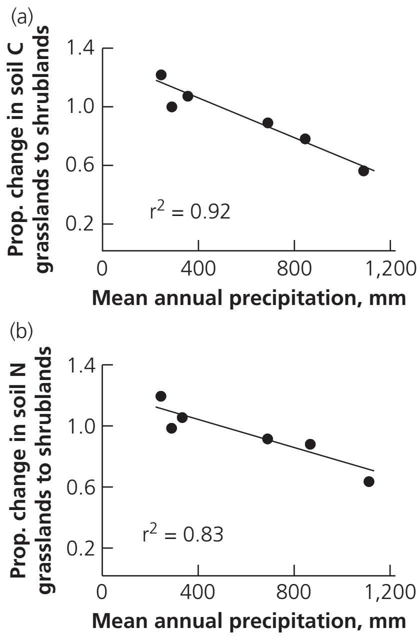

Fig. 10.21 Jackson et al. (2002) found a negative correlation in (a) soil organic carbon and (b) nitrogen budgets between six pairs of adjacent grasslands in the Chihuahuan Desert (North America) in which one of each pair of grasslands was invaded by woody vegetation 30–100 years ago.

Source: From Jackson et al. (2002). With kind permission of Nature Publishing Group.

10.3 Pumping aquifers: a problem of less water and more salinity

Some of the most obvious effects of aquifer pumping occur in desert golf courses (Wheeler and Nauright 2006). The negative effects are widespread, and include a more general problem of reduction in groundwater. In addition, high fertilization and insecticide levels are needed to keep the courses green (Wheeler and Nauright 2006). The use of the water from the Colorado River for urban purposes in southern California has resulted in the river no longer reaching the sea in the arid Baja peninsula, Mexico.

The use of water in deserts varies tremendously, with greater use by high-income families in Namibia (Jacobson et al. 1995) (Fig. 10.22). Additional negative effects of groundwater depletion are found in many desert areas. For example, Lamoreaux et al. (1985) found that exploitation of groundwater for irrigation in the Kharga Oases of the Western Desert of Egypt from springs as well as from shallow and deep artesian wells has caused severe declines and even termination of groundwater extraction from certain wells. By 1975, many deep wells had stopped flowing, and shallow wells were also being pumped. The major problem, in Lamoreaux et al.'s (1985) view, is that wells are placed too close to one another and are poorly managed. Dabous and Osmond (2001) found that, in the Western Desert (Sahara), the observed lowering of groundwater is caused not only by pumping at a rate greater than inflow from the aquifer systems, but also by the withdrawal of pluvial water which is not being replaced.

One of the world's worst desertification areas is the Aral Sea region, which includes part of the Turkestan Desert (Saiko and Zonn 2000). During the 1960s, a large-scale irrigation campaign attempted to improve cotton production in Soviet Central Asia. From 1960, ever-increasing water withdrawal from the two inflowing rivers, the Amudarya River and Syrdarya River, has resulted in the dramatic decline in the size of the sea. Desiccation was accompanied by the development and further acceleration of various desertification processes. Saiko and Zonn (2000) found that, for different reasons, the predominant direction and trends of desertification have been changed dramatically from 1961 to 1995 (Figs. 10.23a–b). In 1950, the total

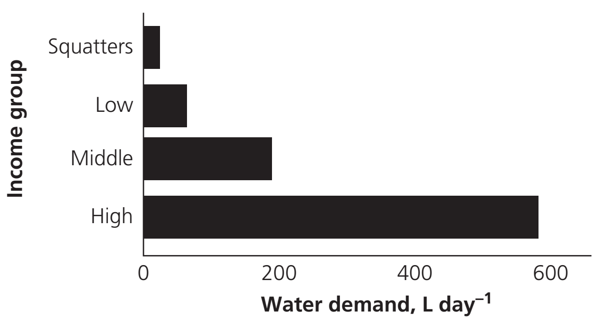

Fig. 10.22 Water use in neighbourhoods in Windhoek, capital city of Namibia. Squatters are people who live in temporary shelters. Mean annual rainfall in Windhoek is about 300 mm.
Source: From Jacobson et al. (1995). With kind permission of the Desert Research Foundation of Namibia.

(a)

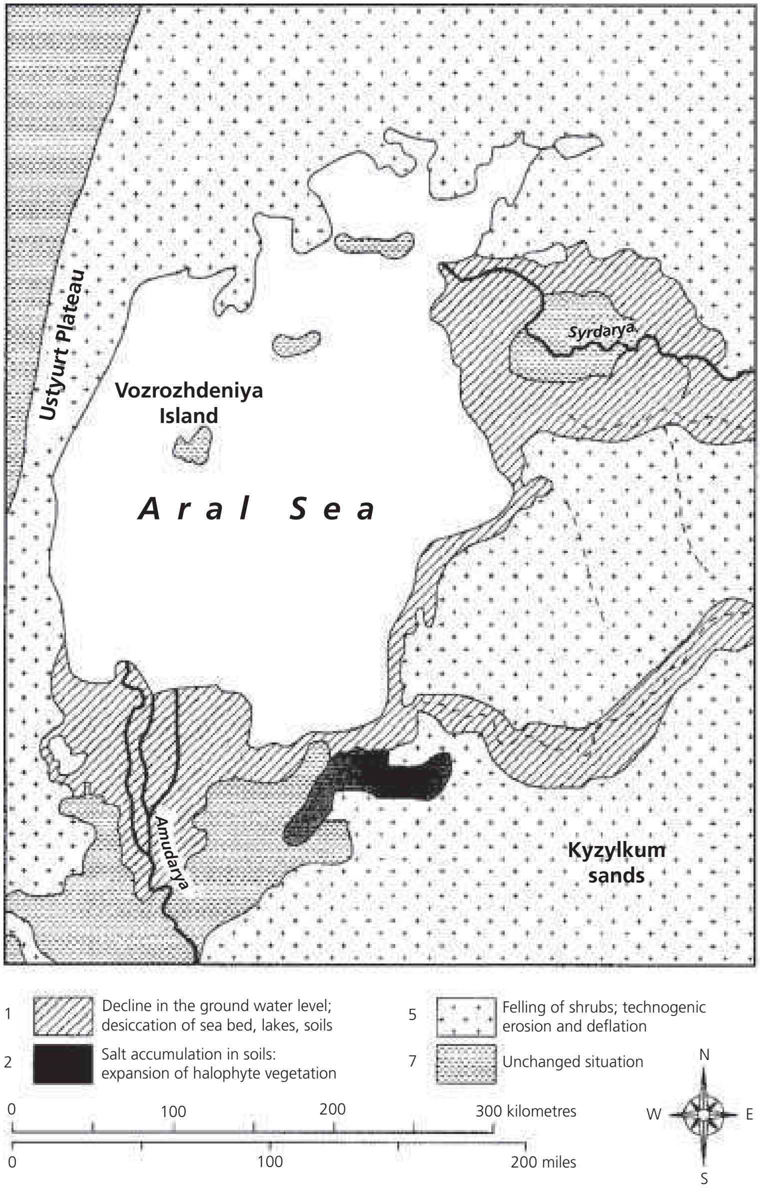

Fig. 10.23 In the Aral Sea region, the predominant direction and trends of desertification have changed dramatically from 1961 to 1995 (a-b). Tugai (6) = riparian forests growing along the rivers in the continental desert regions of central Asia.

Source: Modified from Saiko and Zonn (2000). With kind permission of Elsevier.

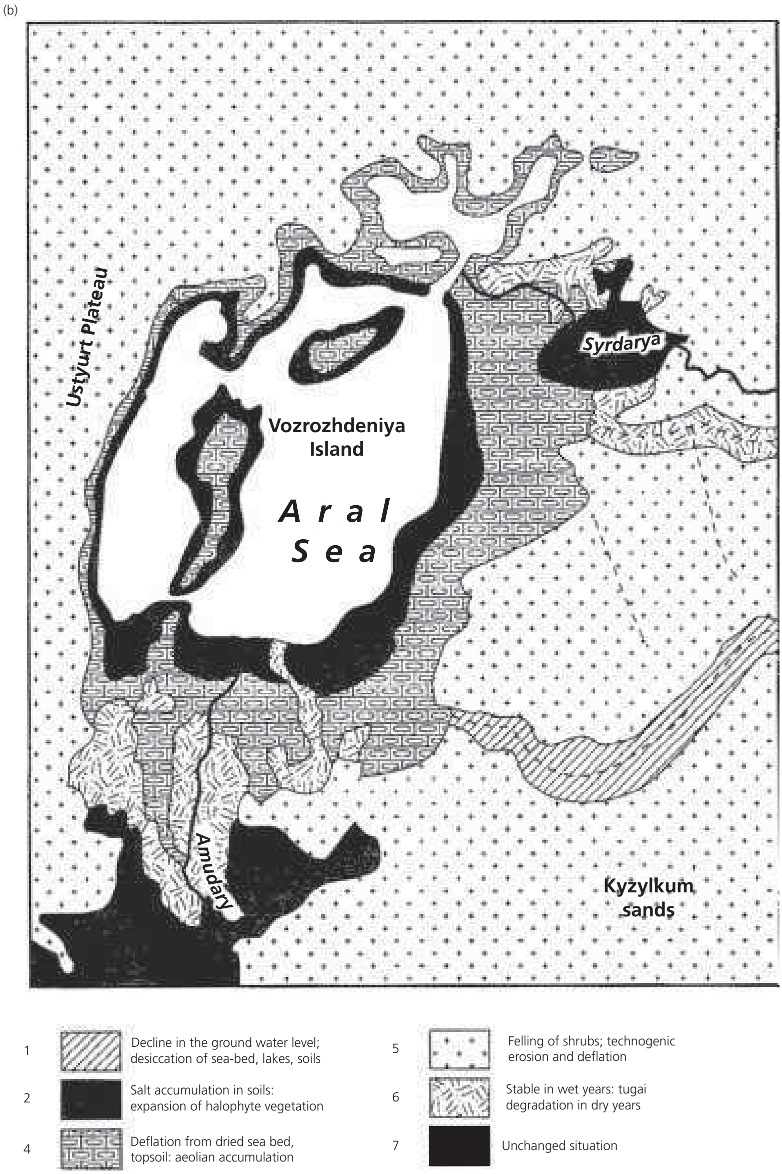

Fig. 10.23 (Continued)

irrigated area amounted to 5.4 million ha of Central Asia. Up to 1965, the rate of irrigation expansion slightly exceeded 0.5% per year. During the next 5-year period, it increased at a rate of over 1% and from 1970 to 1975 it was 2% per annum (Zonn 1993). However, expansion was particularly rapid during the next 13 years, when the area of irrigated land in Central Asia reached 9.4 million ha, showing an increase of 70% for the region as a whole. The area of irrigated land within the Aral Sea basin was estimated at close to 8 million ha (Saiko and Zonn 2000). The total area of the Aral Sea declined from 66,900 km^2 in 1960 to 32,000 km^2 in 1995 and the salinity of the sea changed from 11–14 to 34 g L^{-1}. The commercial fish catch from the Aral Sea changed from 30–40,000 t $year^{-1}$ to no catch at all. The main causes of desertification of the Aral Sea were the decline in the groundwater level, increased mineralization and chemical pollution of watercourses, soil salinization, the spread of xerophytic and halophytic vegetation, and deflation and aeolian accumulation, with the development of salt storms (Saiko and Zonn 2000).

10.4 When is it desertification? The importance of reversibility

Many causes of desertification have obvious solutions. For example, in California, the baseline for comparison of water use on golf courses is the amount of growth that a crop would have, multiplied by 0.80 (Green 2007). Now, it is well known that monocultures have a far higher water use than desert ecosystems. Thus, comparing water use in a crop plant to the amount of water a golf course may use is not a valid comparison because it exaggerates the values for natural vegetation. The real comparison in desert regions should be with a natural desert ecosystem, where shrubs are 'islands of fertility' surrounded by areas with few or no plants (Ravi et al. 2010). Similarly, effects of soil salinization, pollution (e.g. Fig. 10.24), agricultural development in marginal desert lands, and housing developments can be directly assessed in terms of their negative effects on the environment.

Fig. 10.24 Oil pollution due to a burst pipe that spilled into Ein Evrona nature reserve near Eilat, southern Israel.

Source: Photo courtesy of Doron Nissim.

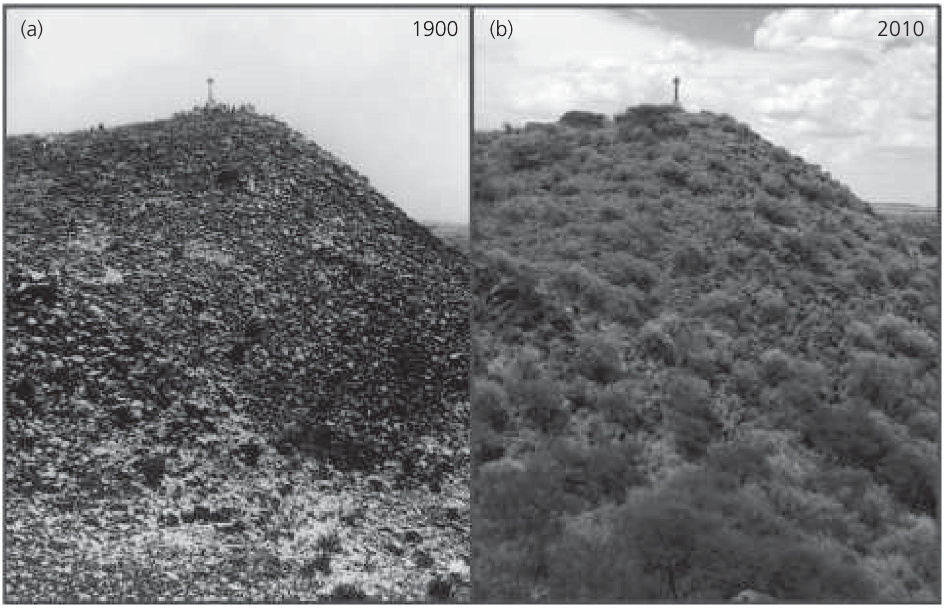

Fig. 10.25 Fixed-point photographs taken of the Highland Brigade memorial at Magersfontein, South Africa. (a) Taken in 1900 by an unknown photographer. (b) Taken in 2010 (8 December) by Hoffman and Ward. They show the change from pure grassland to savanna, with *Acacia tortilis* in the foreground and *Tarchonanthus camphoratus* in the background on the hillside.

Source: From Ward et al. (2014). With kind permission of Taylor and Francis.

Another example comes from rangeland studies, which are largely based on changes in vegetation. See, for example, Figs. 10.25a and b from the 2nd Anglo–Boer War battle site of Magersfontein (South Africa). Figure 10.25a was taken at the time of the erection of the Highland Brigade memorial in 1900 and the same photograph in Fig. 10.25b in 2010 (Ward et al. 2014). In another study, Rohde and Hoffman (2012) found that patterns of change in Namibian arid rangelands were correlated with rainfall. Below a threshold of 250 mm, vegetation has remained relatively constant regardless of land use. They found that above the threshold of 250 mm mean annual precipitation (which is mostly rain), an increase in rainfall led to an increase in tree cover. They also recognized that there were effects of land-use transformations (including decimation of megaherbivores such as elephants and fire suppression) and increased global carbon dioxide concentrations.

11 Conservation of Deserts

11.1 Are deserts worth conserving?

Hopefully this book has managed to convince you that deserts are superb evolutionary laboratories of nature. For that alone, they merit conservation. Deserts are particularly well suited for the study of evolutionary changes in species. There are many additional reasons for why it is important to conserve deserts, for example:

1. Unique features of desert species and habitats;
2. Ecological benefits provided by these habitats; and
3. Because many desert areas have historically been perceived as wastelands, many are in relatively pristine condition (but see Chapter 10 for negative human impacts on desert habitats).

Conservation can be carried out using many different approaches. Here we consider the following:

1. Is it more worthwhile to conserve individual desert species or is it more appropriate to follow a habitat-level approach?
2. Reintroductions and recolonizations of endangered species and revegetation of desert habitats may be important in certain environments.
3. In areas where there are strong genotype by environment ($G \times E$) interactions—that is, where evolution of new species starts to occur—it may be important to conserve each population separately.
4. Lastly, this chapter considers the institutional means of controlling desert habitats and whether we can afford such habitat conservation.

11.2 Conservation of desert species or habitats

Conservation can focus on a single species, with an emphasis on umbrella species, keystone species, focal species, or indicator species (Cohn 2001). The term umbrella species infers that by saving a single species, one saves a lot of other species that are 'under the umbrella'. These are usually large species with low reproductive rates and

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large home ranges (Mills et al. 1993; Berger 1997). Keystone species are those species that play a disproportionately important role in the ecosystem and therefore saving them may save many other species that depend on them (see Chapters 5 and 6 for examples of such species). Focal species are those that have a high perceived value for conservation because they are aesthetically pleasing and conserving them will usually serve to conserve a lot of habitat, and consequently lead to the conservation of other species. Indicator species are considered to be useful for conservation because they are indicators of particular conservation priorities. In all four cases, it is clear that saving any of these species necessarily leads to saving a number of other species that either depend on them (e.g. keystone species) or happen to occupy the same habitats (e.g. umbrella, focal, and indicator species).

11.2.1 Umbrella species

Berger (1997) considered the value of the Namib Desert-dwelling black rhinoceros, *Diceros bicornis* (Fig. 11.1), as an umbrella species. This is the only unfenced population of this species with more than 100 individuals (Berger 1997). He examined the value of conserving this species relative to the conservation of six large herbivores ranging in size from the giraffe, *Giraffa camelopardis*, to springbok, *Antidorcas marsupialis*, and the ostrich, *Struthio camelus*. He found that all species, with the exception of the black rhino, moved according to rainfall variation. Such large changes in population sizes meant that, at best, only populations of about

Fig. 11.1 Black rhino in northern Namibia.
Source: Photograph courtesy of Alastair Rae.

250 animals would be conserved in the area (about 7,000 km^2) of the Kaokoveld of the Namib Desert where the black rhinos occurred (Fig. 11.2). One-third of the species never had populations >50 individuals. One of the assumptions regarding suitability as an umbrella species is that black rhinos must be a viable population, and 50 individuals is often considered to be the 'magic' effective population size (N_e) for conservation of populations in the short term (~5 generations) (Franklin 1980; Soulé 1980). N_e differs from the censused population size because N_e is the number of reproductively active individuals contributing to the next generation (Soulé 1980). This number of 50 is the number of individuals needed to avoid problems related to inbreeding depression (Jamieson and Allendorf 2012). Indeed, Frankham et al. (2014) consider that a number closer to 100 individuals is needed to effectively conserve a population. Berger (1997) was most concerned that desert-dwelling black rhinos are not necessarily viable, largely because of poaching. Indeed, Berger and Cunningham (1994) considered the fact that black rhinos are dehorned by the wildlife authorities in Namibia, Zimbabwe, and Swaziland in an attempt to reduce poaching because these large animals are poached for their horns. They found that female black rhinos lose all their infants when there are dangerous carnivores such as spotted hyaenas (*Crocuta crocuta*) and lions (*Panthera leo*) in the area and lose none of their infants when there are no dangerous carnivores. However, Berger and Cunningham (1994) recognized that dehorning resulted in lower mortalities (33%) for inter-female rivalries. They concluded that dehorning could be a valid conservation strategy only where dangerous carnivores were excluded.

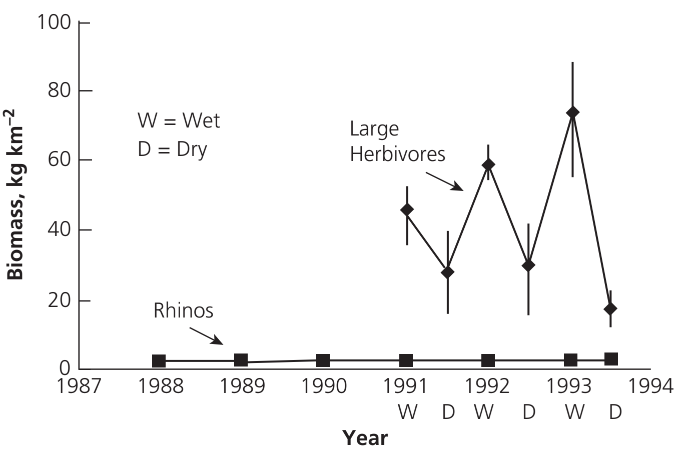

Fig. 11.2 In the Kaokoveld region of the Namib Desert where the black rhinos occurred, about 33% of the large herbivore species never exceeded populations of more than 50 individuals. Black rhino populations were also too small to be useful indicator species.

Source: From Berger (1997). With kind permission of Blackwell.

11.2.2 Keystone species

I discussed a number of examples of keystone species in Chapters 5 and 6. They have an importance that is in excess of their abundance. Examples include the African and Middle Eastern *Acacia* species. Another example of a keystone species is the camel, which because of its large size has a key role in the germination of *Acacia* species. Another keystone species is the elephant (Fig. 11.3), which plays a major role by pulling down large trees, making them available to shorter herbivores, particularly in the Namib Desert. Other keystone species include lions, spotted hyaenas, dingoes, and coyotes (Chapter 6) because of their important roles as keystone predators.

Fig. 11.3 Desert elephant in arid Namibia.

11.2.3 Focal species

Beier (2009) noted that, as habitat areas are fragmented and lost due to increasing human use of the landscape, focal species are the first species to suffer. Of these, the cougar (*Puma concolor*) plays a significant ecological role in the deserts of North America. In addition to being highly sensitive to an area, cougars are sensitive to human activities that can degrade the utility of buffer zones and corridors. For example, although cougars use culverts and other road-crossing structures, a cougar walking in a drainage bottom climbed out of canyons to cross multi-lane roads. Thus, cougars can be a useful focal species to ensure that a conservation plan includes roadside fencing that funnels animals to crossing structures. Because dispersing cougars are sensitive to artificial night lighting, the cougar is also a useful focal species for minimizing artificial night lighting in wildlife corridors. Cougars may also be a useful focal species for minimizing the effects of anticoagulant poisons, either as secondary consumers (i.e. after eating animals that had previously consumed poisons) or as tertiary consumers (i.e. eating animals that had eaten animals that had consumed poisons). Cougars are obviously an appropriate focal species for efforts to manage an endangered population, reintroduce cougars, or facilitate recolonization. There are advantages to using cougars as a focal species for designing wildland networks and linkages. However, large carnivores such as cougars are not appropriate to use as the sole focal species because they may have peculiar dietary and habitat demands that may differ from those of other species.

Beier and Brost (2010) and Brost and Beier (2012a) proposed an alternative approach based on land facets (recurring landscape units of relatively uniform topography and soils) that complements the use of focal species for making conservation decisions. The rationale is that corridors with high continuity of individual land facets will facilitate movement of species associated with each facet today and under changed climates in the future. Conservation practitioners might like to know whether a linkage design based on land facets is likely to provide continuity of modelled breeding habitat for species needing connectivity today, and whether a linkage for focal species provides continuity and interspersion of land facets. To address these questions, Brost and Beier (2012b) compared linkages designed for focal species and land facets in three landscapes in Arizona, U.S.A. They used two variables to measure linkage utility, namely distances between patches of modelled breeding habitat for 5–16 focal species in each linkage (including cougars, Sonoran desert toads (*Bufo alvarius*), desert tortoises (*Gopherus agassizii*), desert box turtles (*Terrapene ornata luteola*), Gila monsters (*Heloderma suspectum*), and Sonoran whipsnakes (*Masticophis bilineatus*)) and resistance profiles (a function of cell attributes in a geographic information system and is usually estimated as the inverse of habitat quality) for focal species and land facets between patches connected by the linkage. Compared to focal-species designs, linkage designs based on land facets provided as much or more modelled habitat connectivity for 25 of 28 species–landscape combinations, failing only for the 3 species with the most narrowly distributed habitat. Brost and Beier (2012b) suggest that, where focal-species designs are possible, the land-facet approach can be used to complement, rather than replace, focal-species approaches.

11.2.4 Single populations

Another conservation issue deals with conserving single populations or metapopulations. One of the most common ways of assessing the viability of single populations is via the use of matrix models (Caswell 2001) in what is known as population viability analysis (Beissinger and McCullough 2002; Brigham and Schwartz 2013; Pe'er et al. 2013). Another more complex approach is to use spatially explicit models (Wiegand et al. 1999, 2000; Jeltsch et al. 2000). A desert example of the use of matrix models comes from Jimenez-Sierra et al. (2007), who studied the candy barrel cactus, *Echinocactus platyacanthus*, in the Tehuacán Desert (part of the Chihuahuan Desert) in Mexico. This species is endemic to Mexico. Tissue from inside the stem is used to prepare a traditional sweet or candy called acitrón, although it is mainly used for forage for goats and donkeys that feed on the flowers and fruits and on those stems that do not have spines. The species is not cultivated in Mexico and so the removal of these plants is entirely from native populations. Jimenez-Sierra et al. (2007) conducted three censuses in six populations during 1997, 1998, and 1999. They found that fruits contained many seeds (about 170 seeds/fruit) and that fecundity increased as plant size increased but that seedling establishment and recruitment were low (2×10^{-6}). The rates of population growth (λ) were close to 1, which indicates that the population is neither declining nor increasing in size, although some populations were declining ($\lambda < 1$). Elasticity values, which are a measure of the sensitivity of the population to changes in individual fecundity, growth, and stasis (some individuals do not change size from one year to the next), indicated that the stasis of the adults contributed most to demography ($S = 0.98$), followed by growth ($G = 0.017$), and fecundity ($F = 0.001$). It had been proposed that barrel and globose cacti (or other species with short lifespans) would have higher elasticity values for growth and fecundity. However, Jimenez-Sierra et al. (2007) found that populations of this species behave similarly to the far larger columnar cactus species such as the saguaro *Carnegiea gigantea* (Steenbergh and Lowe 1977), *Neobuxbaumia tetetzo* (Godínez-Alvarez et al. 1999), and *Neobuxbaumia macrocephala* (Esparza-Olguín et al. 2002), in that stasis was the most important feature of population demography. Jimenez-Sierra et al. (2007) concluded from these studies that the protection of adult *Echinocactus platyacanthus* plants was most important for the conservation and management of this species. The conservation of these plants can only be maintained if the removal and destruction of large adults is stopped, especially because larger individuals produce more seeds. Among the methods that Jimenez-Sierra et al. (2007) consider will be useful for this species' conservation include (1) the establishment of grazing-free areas where competition with other shrubby species is minimized, (2) the collection and storage of seeds from areas that have deteriorated or have been subjected to heavy grazing pressure, and (3) the cultivation of the cactus in greenhouses by local inhabitants.

In spatially explicit models, Wiegand et al. (1999) and Rodriguez-Perez et al. (2011) studied the factors affecting the distribution of *Acacia raddiana* in the Negev Desert of Israel because of the concerns expressed for their conservation by Ward and Rohner (1997) (see Chapter 10). They evaluated the relative importance of different processes such as seed production, seed infestation by bruchid beetles, germination, mortality, and infestation by the hemiparasitic mistletoe *Plicosepalus acaciae* for the survival and recruitment of *Acacia* trees in the Negev Desert. The most important factors affecting mortality rates at different life stages were the production of uninfested seeds (Rodriguez-Perez et al. 2011) and the weather regime. The infection of trees by hemiparasitic mistletoes proved to be of minor importance. The most important result Wiegand et al. (1999) found was that an increase in the germination rate of *Acacia* seeds is capable of counteracting the detrimental effect of unfavourable climatic conditions and the negative effects of seed infestation by bruchid beetles (Bruchidae). This may result from the mechanical effect of passage through the gut of large mammalian herbivores, because of scarification by the hydrochloric acid in the digestive tract. Bodmer and Ward (2006) showed that the larger the herbivore, the greater the probability of germination (Fig. 11.4; see also Chapter 7) and recommended that

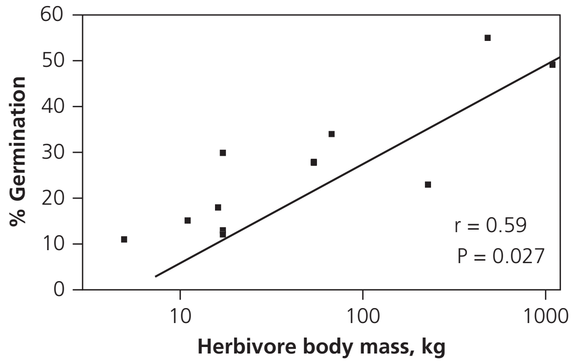

Fig. 11.4 Positive relationship between % germination and mammalian body size. The mechanism is that seeds remain in the gut of large mammals for longer than in small mammals.

Source: From Bodmer and Ward (2006). With kind permission of Cambridge University Press.

camels be brought in to maximize germination probability. Camels also consume young seedlings, so they would need to be removed before the plants reached the seedling stage. Consequently, Rodriguez-Perez et al. (2011) recommended the use of increased large mammalian herbivore densities as a possible management option for enhancing the survival of *Acacia* populations in the Negev (Fig. 11.5).

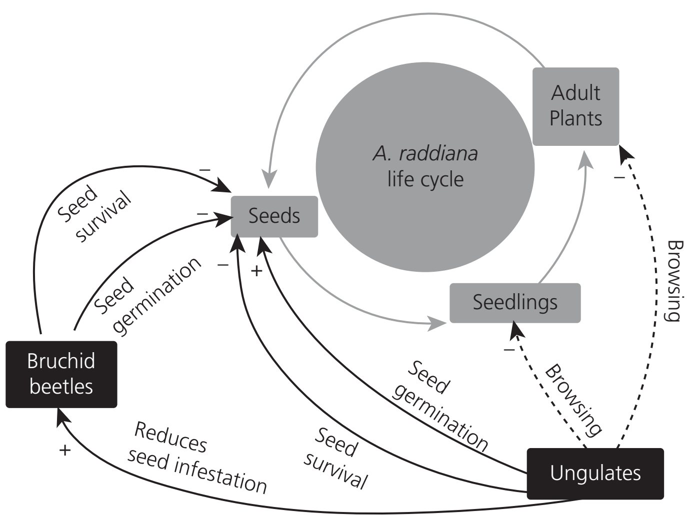

Fig. 11.5 Diagram showing the factors affecting *Acacia raddiana* regeneration without (black solid lines) and with herbivory (black solid plus dashed lines). Plant life stages (grey boxes and arrows) are affected by plant–animal interactions (i.e. bruchid beetles and ungulate herbivores) which can have positive (i.e. arrows with '+' sign) and negative effects (arrows with a '-' sign) on plant fitness. 'Browsing' indicates consumption of tree parts by ungulate herbivores.

Source: From Rodriguez-Perez et al. (2011). With kind permission of Springer.

11.2.5 SLOSS or metapopulations

The debate over single large or several small (SLOSS) habitats has long been an issue for discussion in the field of conservation. The debate deals with fragmented habitats and whether it is better to conserve one large habitat of a given size or to split it into several small habitats of the same size. This follows on from the dynamical theory of island biogeography of MacArthur and Wilson (1964). Primack (2006) considers the best reasons for conserving a *single large* habitat to be the fact that the number of species conserved increases (usually) with area ($S = cA^z$, where S = species richness, A = area conserved; c and z are positive fitted constraints where z lies between 0 and 1), there are fewer negative consequences of edge effects, and it will preserve more species that happen to have large habitat requirements (e.g. elephants or lions). On the other hand, the benefits of conserving *several small* habitats of the same size may be that it could be easier to increase the diversity of habitats protected because they are spread out over a considerable distance, there would be a lower probability that any population might be eliminated by stochastic events such as disease or a similar catastrophe, and it may be easier to convince people with competing interests to implement conservation efforts (e.g. for housing or agricultural developments). Primack (2006) proposed that the best of both worlds would be to have a group of large and small habitats that are connected by corridors or stepping stones because this would create metapopulations of protected species. Metapopulations, which are multiple populations of the same species that are connected through immigration and emigration (Levins 1969; Pulliam 1988), are clearly important to conserve because sometimes a single population may go extinct for reasons that are unclear or because the population happens to be a 'sink' population. For example, the desert lily *Pancratium sickenbergeri* in the Negev Desert (Israel) occurs in high densities in sand dunes but occurs at low densities in associated dense loess-sand habitats (Ward et al. 2000a). One might conserve the high-density population because this should be where they stand the best chance of survival and reproduction. However, the sand dune populations are 'sink' populations as they have very high mortality of flowers (1:30,000) and no vegetative reproduction, while the loess-sand populations are 'source' populations where there is some reproduction and dispersal occurs to the 'sink' populations (*sensu* Pulliam 1988; Ward et al. 2000a). Without the 'source' populations, 'sink' populations would go extinct in a few years (Ward et al. 2000a).

Shkedy and Saltz (2000) considered the metapopulation dynamics of the Nubian ibex, *Capra ibex nubiana* (Fig. 11.6), a species of rocky cliffs in the Middle Eastern deserts. They used 20 years of data from the Israeli Nature Reserves Authority records, with some 1,650 observations. They found that there were three core zones in the Judean and Negev deserts (Israel) and that these were joined by corridors linking them. There were core areas in the Judean Desert (about 1,000 animals on the west coast of the Dead Sea), the Negev highlands (about 500 animals), and the Eilat mountains region in the south (about 150 animals) (Fig. 11.7). Corridors were more likely to be flatter than core areas, presumably because ibex must move rapidly and directionally between core zones. Shkedy and Saltz (2000) considered that

Fig. 11.6 Nubian ibex in the Negev Desert.

Source: Photo courtesy of Alon Ziv.

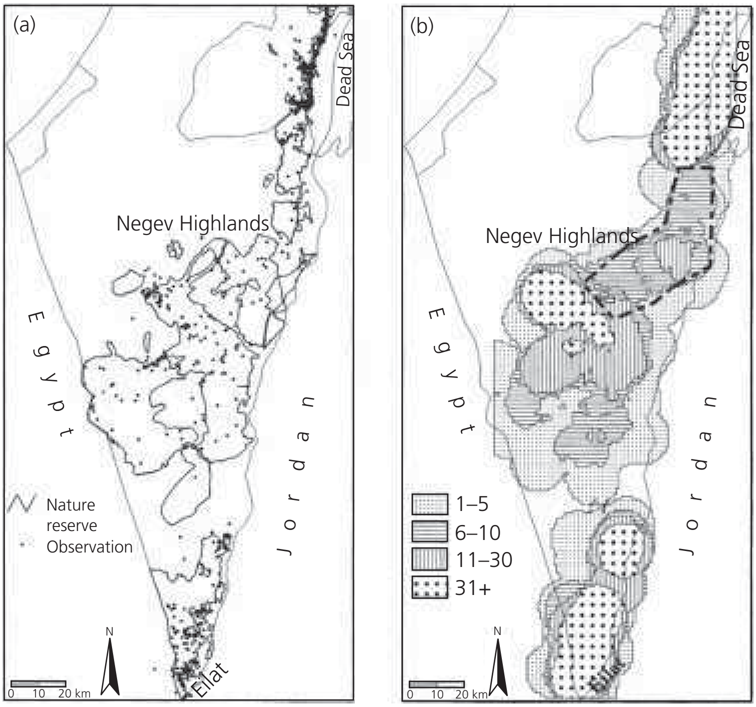

Fig. 11.7 Map of the core areas for Nubian ibex in the Judean Desert (north, near Dead Sea), the Negev highlands, and the Eilat mountains region in the south. Numbers in (B) indicate numbers of animals seen.

Source: From Shkedy and Saltz (2000). With kind permission of Blackwell.

the extensive fencing of the international borders between Israel and Jordan and between Israel and Egypt may curb the passage of ibex between the southern Eilat Mountains and the central Negev highlands populations. They considered this species to be a potential umbrella species and that conserving metapopulations of this species could also aid in the conservation of other rock-dwelling species such as the Syrian hyrax (*Procavia syriaca*), Afghan fox (*Vulpes cana*), and leopard (*Panthera pardus*).

11.2.6 Conserving the entire habitat

There are problems associated with conserving large areas. For example, there is the SLOSS debate described in the previous section and the issue of global warming. Global warming may lead to increases in the sizes of desert habitats or may lead to decreases in the habitats suitable for particular species (Saltz et al. 2006; Foden et al. 2007; Midgley and Thuiller 2007).

One of the most important desert biomes to conserve is the Succulent Karoo of southern Africa (South Africa and Namibia), which occurs on the arid fringes of the Cape Floristic Province. The Succulent Karoo is the only arid habitat that is considered a hot spot of biodiversity. It includes 4,850 plant species of which about 40% (1,940 species) are endemic (Ihlenfeldt 1994; Hilton-Taylor 1996). This is particularly due to the rapid diversification of the Mesembryanthema (part of the family Aizoaceae, also known as ice plants) (Klak et al. 2004). Both local (α) and regional (γ) diversity are high. On average, about 70 species have been recorded in a single 0.1-ha plot, with a maximum α diversity of 113 species, a diversity that is exceeded only in the Negev Desert (Ward and Olsvig-Whittaker 1993; Ward et al. 1993). However, regional diversity in the Succulent Karoo is extraordinary and is about four times higher than that in any other winter-rainfall desert in the world (Cowling et al. 1998). For example, in the mountainous Gariep section of this habitat, 331 plant species have been recorded in 1.3 km^2 in an area where annual rainfall is less than 70 mm (Von Willert et al. 1992). This high regional species richness of plants in the Succulent Karoo is caused by great compositional change in environmental and geographic gradients, especially with regard to edaphic specialists with limited distributions. Endemism is particularly common among succulents (especially Mesembryanthema (Aizoaceae)) and bulbous plants and is focused on hard substrates such as quartzites, quartz-gravel plains, and shale ridges (Schmiedel and Jürgens 1999). There are 851 Red Data Book species in this biome (indicating threatened, vulnerable, and endangered species; Hilton-Taylor 1996).

Cowling et al. (1999) have proposed a spatial scheme for the preservation of this region's biodiversity that maximizes the retention of species and allows for their persistence. By substituting space as surrogates for ecological and evolutionary processes, they consider it possible to achieve a system that combines retention and persistence of biodiversity. They compared the representation of species in the Red Data Book of plant species with their similar-sized system designed for both retention and persistence. The system designed for retention and persistence conserves considerably fewer Red Data Book plant species (37%), which indicates that including a design for persistence (e.g. to adjust for predicted changes in species' distributions caused by global climate changes as mentioned earlier and in Chapter 10) incurs a cost in terms of representation. However, this conservation system is predicted to persist in the face of global climatic changes by, for example, preserving altitudinal gradients of plant diversity (many species change rapidly along edaphic gradients; Cowling et al. 1999; Fig. 11.8) that allow for the maximization of plant diversity across very short distances and should protect many plant species even if global climate changes would change their distributions.

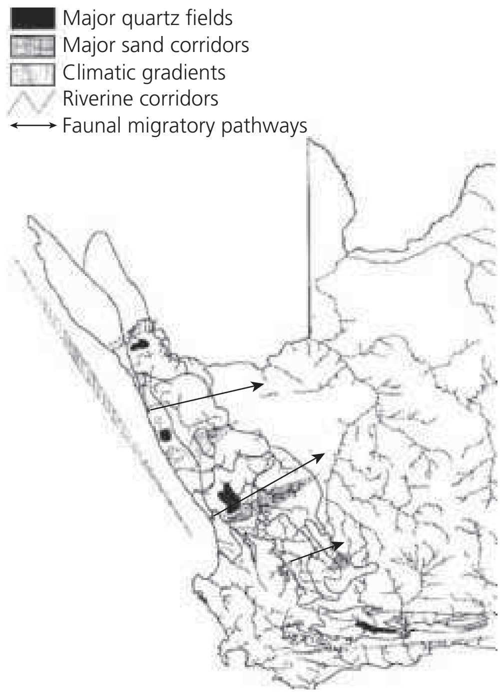

Fig. 11.8 Preserving altitudinal gradients (arrows) of plant diversity in the Succulent Karoo.
Source: From Cowling et al. (1999). With kind permission of Blackwell.

11.3 The 3 Rs: reintroduction, recolonization, and revegetation

Reintroductions of species occur where they have previously been eliminated from the wild or have declined to very low numbers. This section will cover the issue of reintroductions of two herbivore species in the Middle Eastern deserts. The first, the Asiatic wild ass (*Equus hemionus*) was reintroduced into the Makhtesh Ramon erosion cirque in the Negev Desert in Israel in the 1950s (Saltz and Rubenstein 1995; Saltz et al. 2000, 2006). The second, the Arabian oryx (*Oryx leucoryx*) was introduced into Oman (Stanley-Price 1989; Spalton et al. 1999), Saudi Arabia (Treydte et al. 2001), and Israel (Gilad et al. 2008). The American black bear (*Ursus americanus*) has naturally recolonized the desert southwest of the United States and Mexico (Onorato et al. 2007). Finally, I consider the issue of revegetation of desert habitats.

11.3.1 Asiatic wild ass

The Asiatic wild ass (*Equus hemionus*; Fig. 11.9) is a medium-sized (200 kg), polygynous species (Saltz and Rubenstein 1995; Saltz et al. 2000, 2006). In some populations, these animals are considered harem breeders, which involves a single male mating with many females (Feh et al. 1994), although this was not the case in the study by Saltz et al. (2000). This species was once common throughout western Asia but was eliminated throughout most of its range with the introduction of modern firearms. The subspecies endemic to the Middle East (*Equus hemionus hemipus*) became extinct at the beginning of the twentieth century (Groves 1986).

Fig. 11.9 Asiatic wild ass in the Negev Desert.
Source: Photo courtesy of Doron Nissim.

In 1982, the Israel Nature Reserves Authority began to reintroduce Asiatic wild asses from a permanent breeding core founded in 1968 from six animals from the Persian subspecies (*Equus hemionus onager*) and five animals from the Turkmen subspecies (*Equus hemionus kulan*) (Saltz et al. 2000). Between 1982 and 1987, 28 animals were reintroduced into the Makhtesh Ramon erosion cirque. The animals were prime-age animals, which was considered to be vital for a successful reintroduction. Initially, there was a single dominant male that took up a territory of almost 20,000 ha of the cirque. Until 1989, reproductive success was low and population growth was slow (Saltz and Rubenstein 1995). Thereafter, reproductive success increased and more than 100 animals were recorded in 1997. As time passed, more and more males took up territories, and territories got progressively smaller (Fig. 11.10). Territories were focused around natural permanent and ephemeral watering points.

Saltz et al. (2000) found that in reintroduced, territorial polygynous species, effective population size (N_e) may be critically small. Their data indicate that N_e may stay very small for several years until population sizes increase, and ultimately depends on the numbers of males because effective population size depends on the number of breeding individuals. Where a population is a harem species, few males reproduce

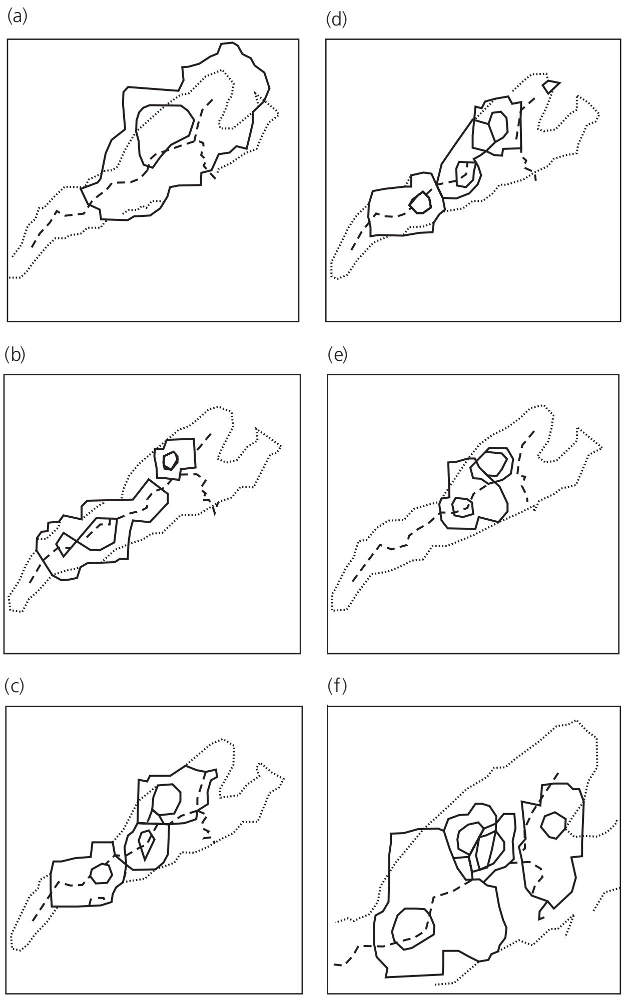

Fig. 11.10 Until 1989, reproductive success of Asiatic wild asses in Makhtesh Ramon erosion cirque was low and population growth was slow. Thereafter, reproductive success increased and more than 100 animals were recorded in 1997. As time passed, more and more males took up territories, and territories got progressively smaller. Dotted line represents perimeter of Makhtesh Ramon. Dashed line represents ephemeral river.

Source: From Saltz et al. (2000). With kind permission of Blackwell.

(most males are bachelor males that do not reproduce). Consequently, the number of breeding individuals is far less than the total number of individuals capable of reproducing. In the case of a single territorial male reproducing and non-overlapping generations, then N_e is 4 because N_e is calculated as $4\,r(1—r)N$, where r is the proportion of males and N is the total population size (Nunney 1993). Doubling the number of females from 11 to 22 would have increased N_e to 6.3 only. By 1995, with 40 breeding animals and five territorial males, and sex ratio at birth of 1:1 and more conventional age structure, N_e was 19.0 for a male survival rate of 0.8 $year^{-1}$ and 25.0 for a male survival rate of 0.3 $year^{-1}$ (note that if male survival is low there is a higher turnover in dominant, territorial males or harem holders, thus increasing N_e–D. Saltz, pers. comm.). Thus, the key feature for conservation strategies regarding this species is to maximize the numbers of male territories. Interestingly, the numbers of males born into this population were strongly male biased in the first years (until 1993) of reintroduction (>2:1).

Consistent with the Trivers and Willard (1973) maternal-allocation hypothesis, females that are in good condition (as these females were) should produce mostly male offspring. The reason for this is that a female maximizes her own genetic output by producing a high-quality male offspring that will mate with many females, thereby increasing her own reproductive output in generations to come. Conversely, young (primiparous) or older females will do best when they produce female offspring because a female offspring (which will not necessarily be of high quality) will produce at least one offspring per annum during her reproductive period (Saltz and Rubenstein 1995). In future reintroductions of this species to other areas, Saltz et al. (2000) recommend introducing prime-age females (as was done in the first reintroduction) to maximize the probability of survival and reproduction but to supplement these introductions with younger (primiparous) females so that the primary sex ratio remains as close to 1:1 as possible.

11.3.2 Arabian oryx

Spalton et al. (1999) recorded the successes and setbacks in the return of the Arabian oryx, *Oryx leucoryx* (80–100 kg), to Oman, which symbolized the success of a new approach to species conservation and established reintroduction as a conservation tool (Stanley-Price 1989) (Fig. 11.11). Ten years after the species had been exterminated in the wild by poaching, the first 10 founder oryx, descendants of the 'World Herd' based in a zoological garden in Phoenix, Arizona, U.S.A., were reintroduced to the desert in central Oman in January 1982. A second release followed in 1984 and the population grew slowly through a 3-year drought that was broken by rain in June 1986. Further years of good rainfall and more founders meant that by April 1990 there were over 100 oryx in the wild, independent of supplementary feed and water, and using a range of over 11,000 km^2. The population continued to grow and by October 1995 numbered approximately 280 in the wild and used over 16,000 km^2 of the Arabian Oryx Sanctuary. However, in February 1996, there was further poaching and oryx were captured for sale as live animals outside the country. Despite the

Fig. 11.11 Arabian oryx in the Negev Desert.
Source: Photo courtesy of Doron Nissim.

poaching, the population continued to increase and by October 1996 was estimated to be just over 400. However, poaching intensified and continued through late 1996 and 1997. By September 1998 it had reduced the wild population to an estimated 138 animals, of which just 28 were females. The wild population was no longer considered viable and action was taken to rescue some of the remaining animals from the wild to form a captive herd.

In Saudi Arabia, Treydte et al. (2001) found that the reintroduction of Arabian oryx has been considerably more successful. There were 17 Arabian oryx reintroduced into the wild in 1990. With a few subsequent additions from a captive herd, by 2000, the population had increased to 346 animals. The animals were reintroduced in Mahazat as-Sayd, a fenced reserve about 2,250 km^2 in area in west-central Arabia, which lies at the periphery of their historical home range (Treydte et al. 2001). The herd managers wished to assess how best to manage the herd, given the constraints that the reserve was fenced, the herd did not have predators and there are large inter-annual fluctuations in primary productivity due to the high coefficient of variation in rainfall. The first two factors meant that the population would reach carrying capacity (K) because there was no predation and because the oryx herds could not move outside the reserve. The last-mentioned source of variability can be a considerable problem because variance in reproductive output has a stronger negative effect on reproductive success than changes in the mean value. Indeed, even if the mean value increases, it is possible for a population to go extinct for random demographic reasons such as founder effects and genetic drift (Ewens et al. 1996). Treydte et al. (2001) modelled strategies of no intervention, constant offtake of 15% per annum, and reducing the herd to 70% of K. They found that the last-mentioned strategy of reducing the herd to 70% of K would be the optimal strategy because it resulted in the least alteration of variance in reproductive success, as predicted by Lande et al. (1995) (see also Saltz et al. 2004 for a similar prediction for desert-dwelling

Hartmann's mountain zebra, *Equus zebra hartmannae*, in Namibia). However, Treydte et al. (2001) recognized that keeping a population at a specific value of *K* would be difficult for managers to implement and suggested that a constant percentage offtake would be possible, albeit at a considerable cost in terms of increased variance in reproductive success, but nonetheless preferable to a strategy of no intervention.

11.3.3 Recolonization by the American black bear

An interesting case of recolonization involves the American black bear, *Ursus americanus* (Fig. 11.12). American black bears have naturally recolonized parts of their former range in the arid Trans-Pecos region of Texas and Mexico after more than 40 years of absence (Onorato et al. 2007). Using microsatellite loci, Onorato et al. (2007) found that these metapopulations were generally panmictic and that there is only moderate genetic structuring of these populations. There is a small population in the Big Bend region of Texas, which is part of a larger population in the Chihuahuan Desert regions of Mexico and New Mexico (United States). Onorato et al. (2007) recommended that close contacts need to be made between Mexico and the United States to ensure that black bears can easily move between the two countries, thereby maintaining genetic homogeneity.

Fig. 11.12 American black bear, taken by remote camera in Sevilleta Wildlife Refuge.
Source: Photo: U.S. Fish and Wildlife Service.

11.3.4 Revegetation

Some of the most effective revegetation schemes have been developed in the People's Republic of China. It is not always clear whether these schemes are involved in vegetating lands that are naturally dune sands and thus do not warrant revegetating because they could be maintained in their natural state or whether revegetation is needed to restore the lands to their original states. In some cases, where key installations such as railways occur, revegetation is needed even though the natural state of the vegetation is indeed desert (see also Whitford 2002). These revegetation techniques involve the creation of windbreaks made from willow or bamboo, followed by the formation of straw checkerboards, allowing time for native xerophytic shrubs to establish (Li et al. 2004). Among these, *Caragana korshinskii, Artemisia ordosica*, and *Hedysarum scoparium* are often planted in the Tengger Desert of northern China (Li et al. 2004). From 1956 to 2001, the development of revegetated areas along the Baotou-Lanzhou railway line was monitored (Li et al. 2004). They monitored β diversity as a measure of species change over time (Fig. 11.13). These researchers found that 40 years after revegetation was started, the probability of new species arriving has declined and has tended towards 12–14 species. Importantly, there has been a change from inorganic soil crusts to a biological soil crust consisting of algae and lichens. However, Li et al. (2004) recognized that there were fewer moss species occurring in the revegetated lands than in naturally fixed dune surfaces.

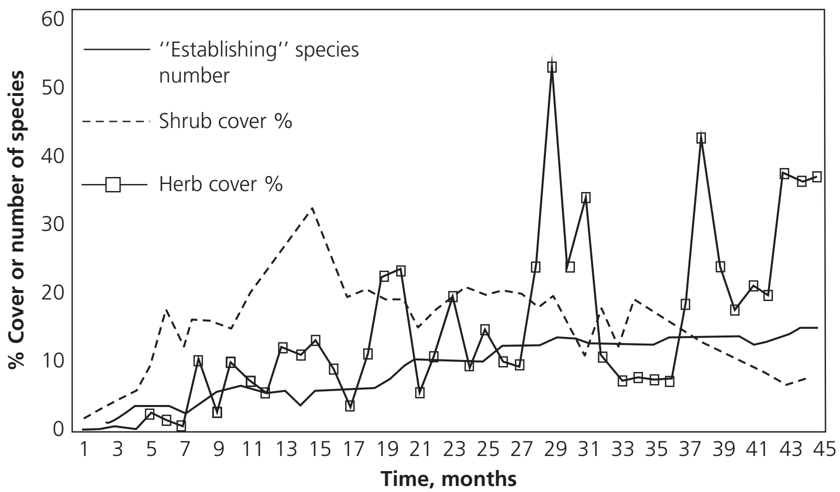

Fig. 11.13 The development of revegetated areas along the Baotou-Lanzhou railway line was monitored (β diversity) as an index of species change over time.

Source: From Li et al. (2004). With kind permission of Blackwell.

11.4 Genotype by environment interactions and intraspecific variability

A number of studies have examined intraspecific variability to determine whether subspecies or variants occur. This is particularly important for conservation because where there are genotype by environment ($G \times E$) interactions, populations should be separately managed (Pfennig et al. 2010; Okubamichael et al. 2011; Murren et al. 2014). Most frequently, this occurs in plant species (see e.g. Rödl and Ward 2002; Bohrer et al. 2003, 2008; Okubamichael et al. 2011 for desert examples), but it has also been described in reintroduced Arabian oryx, *Oryx leucoryx* (Marshall and Spalton 2000).

Okubamichael et al. (2011) examined the level of host specificity in a mistletoe, *Viscum rotundifolium*, in the arid Kalahari of South Africa. There were nine potential host species that this mistletoe could parasitize. However, they found that this mistletoe mostly parasitized two host species, *Ziziphus mucronata* and *Ehretia rigida*, despite the fact that other potential hosts, such as *Tarchonanthus camphoratus* and *Acacia mellifera*, were far more abundant. They performed reciprocal transplant experiments of the mistletoe *Viscum rotundifolium* on three populations of *Ziziphus mucronata*. These populations occurred within about 50 km of each other. They found that survival declined precipitously when the mistletoes were placed on non-local hosts of the same species, *Ziziphus mucronata*. This indicates that there is a genotype by environment interaction, showing that local adaptation was occurring over a very small spatial scale.

Volis and Blecher (2010) have used the widespread observation of local adaptation in many plant populations to demonstrate how *in situ* and *ex situ* conservation can be performed. The conceptual scheme of this strategy is shown in Fig. 11.14.

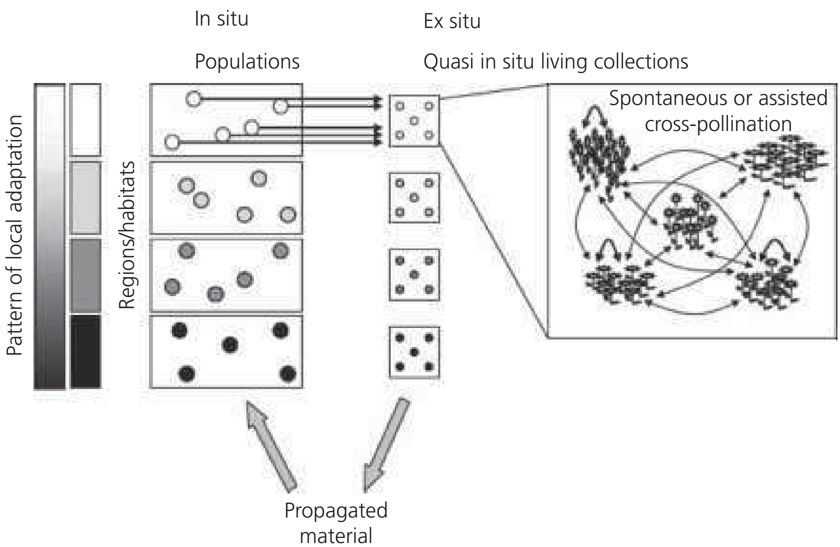

Fig. 11.14 A conceptual scheme of the proposed complex *in situ*–*ex situ* conservation strategy.
Source: From Volis and Blecher (2010). With kind permission of Springer.

They suggest the following five steps to plant conservation when there is significant local adaptation of a species to certain habitats:

(1) Survey and analysis of the distribution of the plant species to identify potentially locally adaptive populations (Fig. 11.15). Two main procedures exist to identify local adaptation: transplantation experiments (e.g. Joshi et al. 2001; Volis et al. 2002) and tests for outbreeding depression, in which locally adapted genotypes are crossed with plants originating elsewhere (Hufford and Mazer 2003). Under local conditions, the progeny from crosses with non-adapted genotypes are expected to have lower fitness due to disruption of co-adapted gene complexes or differential adaptation to environmental conditions. If local adaptation is important, the introduced genotypes must be matched to the local biotic/abiotic conditions; i.e. they should come from the area;
(2) Sampling populations according to a spatially/ecologically structured design to ensure appropriate sampling;
(3) Planting in appropriate sites (i.e. in sites with natural or semi-natural habitats with a close environmental match) and maintaining the collections. A practical recommendation by the Center for Plant Conservation in the United States (Maunder et al. 2004) suggests that the number of plants per population should

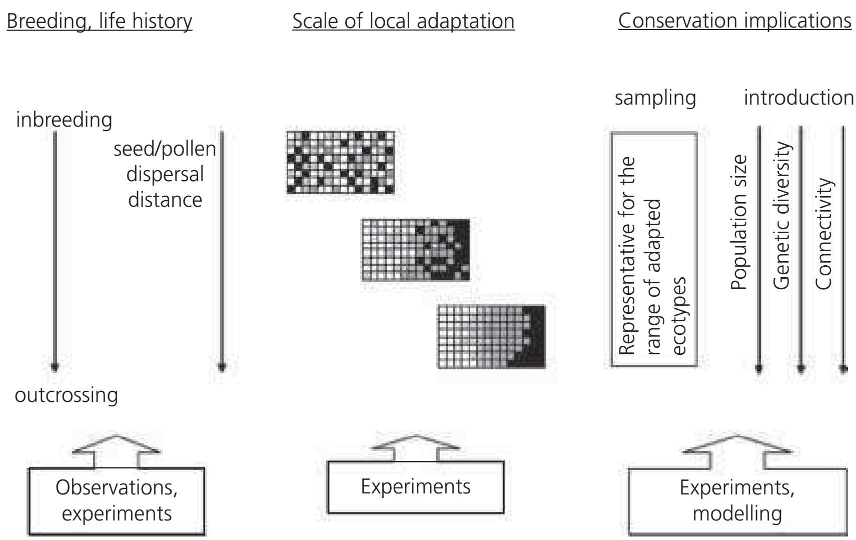

Fig. 11.15 A scheme of the relationships between (i) species properties (breeding structure, life history) and (ii) scale of local adaptation, and implications of (i) and (ii) for sampling and introduction. The scheme shows that predominant outcrossing and large dispersal distance are associated with large-scale local adaptation, necessitating increased size, genetic diversity, and connectivity of introduced populations.

Source: From Volis and Blecher (2010). With kind permission of Springer.

be 10–50, and five or more populations per habitat/eco-region should be sampled. In the quasi *in situ* approach recommended by Volis and Blecher (2010), site choice must take local adaptation (tested or presumed) into account. This means that there must be a close environmental match of the *ex situ* location and locations of sampled natural populations;

(4) Studying life-history traits and abiotic/biotic effects on population demography; and

(5) Reintroduction (or relocation) of plants, preferably using seeds from the living collections, and monitoring of relocation success.

Volis and Blecher (2010) believe that such a strategy is most important to apply to populations that are already declining in their native environments and/or represented by a small number of existing populations.

11.5 Who gets to pay for this conservation and how is it controlled?

There are major differences in the ways that people can control land. For example, in Israel there is no private land ownership, whereas in the United States private land ownership is very common, although there are large swaths of land controlled by the Bureau of Land Management (which allows ranchers access for their livestock under certain conditions) and the United State Fish and Wildlife Service. The ways in which people perceive their abilities to control land access vary enormously. For example, Richer (1995) estimated the benefits of restricting the uses of 2.8 million ha of desert land and creating three new national parks and 76 new wilderness areas in the high and low deserts of eastern California (United States). In a 'willingness to pay' survey, California residents indicated that they would be willing to pay $177 million to $448 million year^{-1} to enact desert protection legislation. This estimate assumed that: (1) the residents who did not complete and return the survey questionnaire ('nonrespondents') would receive no benefits from desert protection, and (2) the estimate of willingness to pay for the 'respondents' is unbiased (Richer 1995). From this study, it is clear that people are willing to pay large amounts of money to protect desert habitats.

11.6 People are also part of the desert environment

It has been stated many times that people (particularly indigenous people) are part of the conservation landscape and need to be considered when conserving landscapes (Gadgil et al. 1993; Berkes et al. 2000; Adams and Hulme 2001; Balmford et al. 2001; Huston et al. 2001; Brown 2003). An interesting example of the role of indigenous people in conservation comes from Australian deserts. It is well known that greater climatic variability tends to increase wildfire size in many arid and semi-arid environments, where alternating wet–dry cycles increase vegetation growth, only to leave a dry overgrown landscape highly susceptible to fire spread. In a study of spinifex areas of the Western Desert of Australia, hunting fires lit by aboriginal Australians have been hypothesized to buffer such variability, reducing the mortality of small-mammal populations. However, these small-mammal populations have suffered declines and extinctions in the arid zone coincident with declines in the numbers of Aboriginal populations. Bird et al. (2012) compared the effects of climatic variability on landscapes dominated by Martu Aboriginal hunting fires with those dominated by lightning fires. They found that Aboriginal fires were smaller, more tightly clustered, and remained small even when climate variation caused huge fires in the lightning region. Bird et al. (2012) considered these effects to likely benefit threatened small-mammal species. Thus, Aboriginal hunters could be considered trophic facilitators, substantially benefitting small-mammal populations. Similarly, Bird et al. (2013) found evidence that burning by Aborigines had a positive effect on one keystone lizard species, the sand monitor (*Varanus gouldii*) (Fig. 11.16). Populations of the sand monitor were larger where Aboriginal hunting was most intense. This effect was driven by an increase in *Varanus gouldii* densities near ecotones. Ecotones were more likely to occur in landscapes that experienced extensive human burning (Bird et al. 2013). Over time, the positive effects of patch-mosaic burning while hunting overwhelmed the negative effects of predation in recently burned areas to produce overall positive impacts on these monitor populations (Bird et al. 2013). These authors recommended that policies aimed at reducing the risk of large fires should promote land-management strategies consistent with Aboriginal burning regimes.

Fig. 11.16 Territorial *Varanus gouldii* in Australian desert.
Source: Photo: Eli Greenbaum.

11.7 Conclusions

Deserts are often perceived as wastelands, and consequently, they are frequently underutilized. Thus, they may be conserved for this reason alone. Although we need to be wary of the potential for desertification, conserving these ecosystems should remain a priority. I believe that deserts make some of the most interesting and compelling places to study evolution in progress. They are also important because of the unique species that occur there and they provide an opportunity to understand biotic interactions because of the relative simplicity of the ecosystems. However, the global changes in climate are causing more areas on desert peripheries to become desertified, which is most unfortunate. Strategies to combat desertification are urgently needed to reverse this trend.

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