Chapter 11
Adaptations to Life in the Namib Desert

Key Concepts and Questions: This Chapter Explains

- *Why the physics of water evaporation, and surface area to volume ratios, are important to survival in hot, arid environments.*
- *What adaptations have evolved in plants and animals to increase water capture and reduce water loss in desert environments.*
- *How desert animals regulate temperature to avoid over-heating through morphological, physiological and behavioural adaptations.*
- *What the role of interspecific competition is in securing resources in food-limited environments.*
- *How a diversity of defence mechanisms protects desert plants and animals from predation.*
- *What hypotheses have been proposed by researchers to explain the 'fairy circles' of the Namib.*

Context: The Namib, A Living Museum of Animal and Plant Adaptations to Aridity

The Namib Desert, most comprehensively represented in **Iona National Park**, is a living museum not only of the geological history of Angola, but also of the extraordinary adaptions (the products of natural selection) that have evolved in animals and plants to survive, grow and reproduce under extreme conditions of aridity and temperature. Responses are exhibited in **morphological, behavioural** and **physiological adaptations.** The outcomes of such long evolutionary processes have fascinated ecologists for many decades, and deserts have become centres of research across the world's hyper-arid zones. In Africa, knowledge of desert adaptations is especially advanced for the Namib biota. Research into the ecology and evolution of desert ecosystems has, for more than 70 years, received a world-renown status through international collaboration at the Gobabeb Namib Research Institute at **Gobabeb** in Namibia. The development of **the Iona-Skeleton Coast Transfrontier Conservation Area**, a collaborative project between Angola and Namibia, has as one of its

objectives the sharing of scientific knowledge and wildlife management experience. Angolan students have a wonderful opportunity to benefit from this partnership.

The breadth and depth of studies undertaken in the Namib exceed those for any other biome represented in Angola and they provide models for many ecological concepts and principles. Dozens of books, and hundreds of scientific papers have been published on the results of research undertaken at Gobabeb, but only a few examples can be illustrated here, drawing from Barry Lovegrove's excellent synthesis *The Living Deserts of Southern Africa* (Lovegrove, 1993, 2021) and Mary Seely's many publications (Hamilton & Seely, 1976; Seely, 1990; Seely & Hamilton, 1976; Seely & Louw, 1980; Seely & Pallett, 2008).

Five key challenges to survival, growth and reproduction in the desert environment serve as a framework for a summary of adaptions: water, heat, food, competition and reproduction.

To these five challenges, one more can be added: wind. In the Namib, wind accounts for sand-blasting, sand erosion, sand deposition and the transport of nutrients from the interior to the coastal dunes, and of fog from the ocean to the land. Wind is the primary factor involved in the formation and movement of hummocks and dunes, in the transport and burying of detritus and seeds, in wind-chill and even as an acoustic signal influencing the activities of dune beetles that can detect the wind from below the sand (Henschel, pers. comm. 2021).

Although exemplified by adaptations for life in the Namib, these factors all demonstrate general principles for life in terrestrial ecosystems.

11.1   Water: The Currency of Life in Desert Environments

Lovegrove (1993) introduces the concept of water as the 'currency of life' to underpin the essential challenge to survival in hyper-arid environments. But all organisms, from the Equator to the Arctic, must regulate the concentration of their body fluids to avoid fatal biochemical imbalances. Mammals cannot lose more than 10% of their body water without resulting in problems due to excessive concentration levels in their bodily fluids. Plants must maintain their water balance to permit the gas exchanges essential to photosynthesis. Water loss takes place through evaporation at the surfaces of animals and plants. Further, in plants, water is lost by transpiration through plant leaf stomata and in animals, during breathing. The rate of water loss is determined by external temperature and water vapour pressure as described in Sect. 5.5.

A fundamental factor in water loss is that of the **surface area to volume ratio**. Small organisms have a higher surface area to volume ratio than larger organisms. A small desert gerbil, weighing 0.1 kg, evaporates 13% of its body weight per hour—17 times faster than a 500 kg camel (Schmidt-Nielsen, 1985). Many Namib plants— such as species of *Adenia, Commiphora, Cyphostemma, Euphorbia, Hoodia*—adapt a short, stout growth form that reduces the surface/volume ratio—the **cauduciform** or **pachycaul** life form (Fig. 5.19). Many desert succulents follow the CAM photosynthetic pathway, opening their stomata and transpiring during the cool of the night.

Some desert trees, such as *Commiphora anacardiifolia* (Fig. 11.1) and *Cyphostemma currorii* (Fig. 11.2) with succulent trunks, have large, fleshy and deciduous leaves, which maximise photosynthetic activity immediately after rain, rapidly storing both carbohydrates and water, thereby being able to endure long rainless periods. Yet others, such as the mopane *Colophospermum mopane* have paired leaves that close together during the midday heat, reducing exposure to the sun's rays. Within the fog belt, the sand-binding grass *Stipagrostis sabulicola* captures fog droplets on it long leaves, which then slip down to the leaf base or fall to the rooting zone of the grass tussock (Fig. 11.3). Some plants reduce leaf architecture to the extreme, as sharp spines, with photosynthetic tissue embedded in their stems, thorns and flowers, as in *Acanthosicyos horrida*, a spiny shrub of the desert dunes (Fig. 11.4).

Two behavioural responses to water scarcity are found in desert plants. Opportunistic species grow fast after unpredictable rains and complete their life cycle—from germination to flowering to setting seeds—within a few weeks. A different

Fig. 11.1 Large-leaved deciduous trees such as *Commiphora anacardiifolia* succeed in the most arid parts of the Namib by exploiting infrequent rain through rapid photosynthesis via their large leaves

Fig. 11.2 Caduciforms such as *Cyphostemma currorii* store water in their succulent trunks *Photo* Ernst van Jaarsveld

Fig. 11.3 Condensed fog droplets on the leaves of the sand-binding dune grass *Stipagrostis sabulicola Photo* Joh Henschel

Fig. 11.4 The melon *Acanthosicyos horrida* has tiny leaves but compensates by having photosynthetic stems, thorns and flowers. Its fruit are a source of food and water for many desert animals. *Photo* Joh Henschel

pattern is found in slow growing and long-lived CAM succulents described above, which can tolerate extended periods of physiological inactivity.

Animals have many adaptations to **reduce water loss** such as the waterproof cuticle of insects, scales in reptiles and the hairy pelage in mammals. Desert reptiles have the lowest water loss rates recorded in animals, about one tenth of that of mammals. Small mammals such as the Namib Golden Mole can regulate their temperature and moisture environment by burrowing under the sand, where they can go into **torpor** while dropping their body temperature. Larger mammals such as springbok make use of the microclimate under shady trees (Fig. 11.5).

The greatest loss of water in animals and plants is during the processes of gas exchange. Animals breath in oxygen and release carbon dioxide; plants take in carbon dioxide during photosynthesis and release oxygen. Section 10.2 describes how grasses and succulents use water efficient C_4 and CAM pathways to reduce water loss during photosynthesis. The gas exchange gateways in plants (**stomata**) have an analogue in insect **spiracles**—an example of the **convergent evolution** of functional adaptations to similar environmental challenges, but within species of very different ancestry. One of the most enigmatic of Namib insects, the flightless

Fig. 11.5 Springbok escaping midday heat under the shade of a mopane (mutiati) *Colophospermum mopane. Note* The horizontal browse-line along the lowest branches of the tree

tenebrionid beetles of the genus *Onymacris*, have fused elytra (the wing covers that open during flight in normal beetles) and which cover the abdominal spiracles. The 'cap' over the spiracles maintains a high humidity, with gas exchange being reduced to a single outlet near the anus. The opening is normally kept closed, except when briefly opened to ventilate the chamber (Fig. 11.6). This adaption for greater water economy came at a cost—the ability to fly.

A regular loss of water in all animals is that which occurs when waste products— faeces or urine—are excreted. These contain energy-rich molecules, CO_2, water and a toxic waste product—**ammonia**. Animals must excrete ammonia in its various forms as rapidly and efficiently as possible. The process requires water. Many desert mammals have specialised kidneys which reduce the volume of water needed in the excretion process by creating a very **concentrated urine**. Short-tailed Gerbils achieve a urine concentration 14 times higher than their blood concentration. It is not
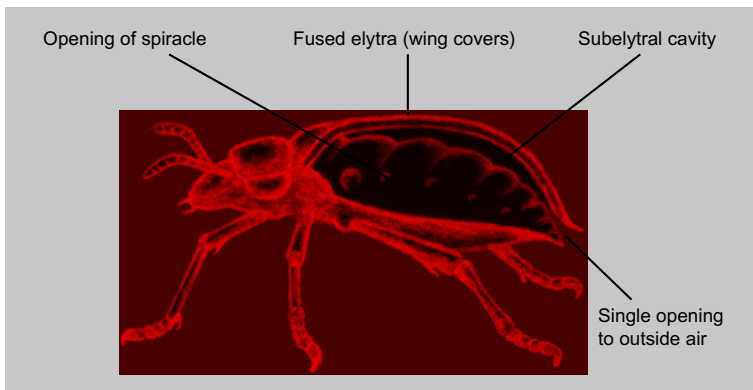

Fig. 11.6   A profile of a typical tenebrionid beetle showing part of the fused elytra, cut away to reveal the sub-elytral cavity into which the abdominal spiracles open for gas exchange. Redrawn from Lovegrove (1993) *The Living Deserts of Southern Africa*. Fernwood Press

only small rodents that must achieve water use efficiency in their bodily functions. The smallest antelope in southern Africa, Kirk's Dik-dik (which was once common in the arid savanna of Iona) has a urine concentration 11 times that of blood. Like Steenbok, also once common in Iona, Dik-dik live independent of any free water sources, selectively feeding on shrubs and grasses at the time of their highest moisture content.

Improving mechanisms of **water capture** is as important to desert biota as their ability to use water efficiently. The coastal Namib, within the zone receiving the cool foggy weather under the influence of the Benguela Current, has many examples of adaptations for effective water capture. Inland of the fog belt, clear, calm nights cause the rapid loss of desert heat, cooling and condensing the air and producing morning dew, a further source of moisture in a region of very limited, unpredictable rainfall. Gemsbok in Iona may be found grazing at night, when the moisture content of the grass *Stipagrostis uniplumis* is 26%, far higher than its midday level of only 9%.

In a narrow margin along the Atlantic coast, **lichens** are unusually common. These cover rocks, sands, shrubs and trees, or simply roll freely over the ground. Lichen are exceptionally well adapted to climatic extremes, reaching their highest diversity and abundance in ecosystems as different as the Namib Desert and the Arctic Tundra. Lichen is a composite organism of algae and fungi forming a **mutualistic relationship**, with different properties to those of the component organisms. Lichens come in many forms, colours and sizes. In the Angolan Namib, especially along the coast between Moçâmedes and Benguela, they are found in foliose, fruticose and crustose forms. During most of the day, they are inactive, presenting the appearance of dead litter. Overnight, they absorb moisture from the fog, initially metabolise using stored energy, and as the sun rises, using solar radiation to photosynthesise in the short time before they once again dehydrate.

Some algal species live entirely below the quartz pebbles that can be found on the gravel plains in many areas of the Namib. The algae utilise the moisture accumulated below the stones, and the light that penetrates the translucent quartz, to photosynthesise. This strange flora is remarkably rich, with over 20 species of green algae and 50 species of diatoms being recorded in the Namib. As Lovegrove (1993) describes, each quartz pebble supports its own **food chain**, with desert arthropods and even snails living off the algae, and desert lizards eating the insects. The organisms that live under these quartz stones are known as **hypolith** communities.

Some Namib plants **capture moisture** from fog directly—their leaves and stalks act as traps down which moisture droplets flow to their roots. Water is also collected by the extensive shallow root systems of the dune grass *Stipagrostis sabulicola* which occupies the bottom of dune slip faces, stabilizing sand movement (Fig. 11.3).

Among desert animals, the Namib **tenebrionid beetle** *Onymacris unguicularis* achieved scientific stardom status in 1976 with cover-page publications in the world's two leading research journals, *Nature* and *Science*. Papers by American researchers Bill Hamilton and Mary Seely (Hamilton & Seely, 1976; Seely & Hamilton, 1976) described studies on the tenebrionid beetles' '**fog basking**' and '**sand trenching'** behaviour. These diurnal flightless dune-dwellers spend the daylight hours foraging for organic litter, retiring at night under a few centimetres of sand of a dune slip-face.

With the cool early morning sunrise, the beetles emerge, climb to the top of the dune crest and take up a headstanding stance. Incoming fog collects on the beetles' shining black backs (the fused elytra previously mentioned), and then rolls down the elytra to be imbibed orally. The beetles increase their body water by up to 34% in this manner. The survival value of this practice is significant. *Onymacris unguicularis* (and *O. bicolor* of Angola, Fig. 11.7) endure long rainless periods through this behavioural adaptation. Populations of other tenebrionid species, lacking this water source, are decimated in such dry spells. Another tenebrionid beetle, the nocturnal *Lepidochora discoidalis*, makes shallow trenches in the sand of sea-facing dunes, trapping fog moisture as a ready source for drinking.

One of the most active carnivores of the Namib, the Brown Hyaena, survives because it is an opportunistic and omnivorous feeder—finding dead seals on the Atlantic shores or dead Gemsbok in the interior. It also feeds voraciously on melons *Citrullus lanatus* and cucumber *Acanthosicyos naundianus*, perhaps more for their water content (up to 90%) than for any nutritional value.

One of the many remarkable research findings in the arid savannas and deserts of southern Africa was that of **water transport** by Burchell's Sandgrouse. South African ornithologist Gordon Maclean found that these desert dwellers often nest up to 60 km from the nearest water source. The **precocial** chicks can run about from the day of hatching, feeding themselves on grass seeds, with their parents not contributing to their feeding. But the chicks are still unable to fly. The male adult flies up to 60 km to the closest water source, soaks his highly absorbent ventral feathers in the pool, collecting up water and flying back to the nest. The water-absorbent feathers are held close to the belly, preventing loss by evaporation during the flight home. Here the young chicks take the still wet feathers in their beaks and strip the water from them.

A common water economy strategy of desert plants is **water storage** in underground bulbs, tubers or aboveground succulent leaves and trunks. **Geophytes** (plants with underground bulbs or rhizomes) are highly sought after by Desert Molerats. They are also excavated by Gemsbok, Porcupine and even small carnivores such as Black-backed Jackal.

Fig. 11.7 The Namib tenebrionid beetle *Onymacris bicolor*, on the dunes at Foz do Cunene. *Photo* Joh Henschel

Water storage is a key property of **pachycauls**, (Fig. 5.19). Pachycauls are especially frequent inland of Lucira, where species of *Commiphora, Cyphostemma, Moringa, Pachypodium* and *Sesamothamnus*, display this growth form. Even more common in the Namib is that of stem and leaf succulence found in many species of *Aloe, Ceraria, Crassula, Euphorbia, Haworthia, Hoodia, Huernia, Sansevieria* and *Stapelia*. The **succulent life form** has evolved independently in many dozens of plant families, but nowhere as abundantly as in the Aizoaceae of the arid zone of southern Africa, where over 35% of the world's succulents are found.

11.2   Adaptations to the Heat of the Desert

A characteristic of desert climates is their clear skies and dry atmosphere, with rapid heating during the day and cooling at night. The surface temperature of Namib desert sands can rise to 75 °C during a summer day, and fall below zero on a winter night. The wide seasonal and diurnal temperature changes are among the many challenges for organisms, which mostly have narrow temperature bands within which to function optimally. Temperature regulation is a critical adaptation in such environments.

A primary physical force in nature is the **cooling power of evaporation**. When water evaporates, the high amount of energy required to break the hydrogen bonds between water molecules is removed from the evaporating surface, resulting in a decrease in surface temperature. Evaporation is triggered by various actions: plants transpire, mammals sweat or pant, birds cool by **gular fluttering**—the rapid oscillation of the floor of their open mouth. Each process is costly in terms of water economy, so many other adaptations have evolved to achieve water efficiency while keeping temperature under control.

Temperature regulation (**thermoregulation**) in animals falls into two types. **Ectotherms** tolerate relatively wide temperature fluctuations and therefore sacrifice the ability to function optimally at all times. Ectotherms include insects, reptiles and amphibians. Their heat is derived from outside sources. Most ectotherms use the sun to warm them to their optimum operational temperatures and regulate energy expenditure. They cannot move about at will as in flying birds or highly mobile mammals. They may either become too hot or too cold, and therefore have to exploit a range of adaptations as described below.

Endotherms can generate heat within their bodies and thus maintain and control a fairly constant body temperature at all times. They can therefore function optimally when and where they choose. Endotherms include mammals and birds. Mammals regulate their temperature between 34 and 38 °C, and birds between 39 and 42 °C. Under cold ambient conditions, their temperature is raised by burning energy until a peak metabolic rate is reached. If the ambient temperature continues to fall, the animal might experience **hypothermia** and possibly die. In hot conditions, cooling is achieved by sweating and evaporation, but this has limits above which the body temperature rises, enters **hyperthemia** (42 °C in mammals, 45 °C in birds) and dies. Despite these constraints, mammals and birds have the freedom to choose where

to live and be active, making them the most thermally efficient creatures on Earth (Lovegrove, 2019).

Animals have two options to deal with deviations from the optimal body temperature—**conform** (ectotherms) or **regulate** (endotherms). Temperature regulation in endotherms can be compared with that of an air-conditioner. A balanced body temperature is achieved through homeostasis. **Homeostasis** is the mechanism by which body temperature is regulated to the desired state (the **set point)** while the external temperature changes. Homeostasis provides a good model of the concept of **negative feedbacks**. The feedback loop includes four steps—the **variable** (body temperature), the **receptor** (nerves, acting like a thermometer), the **integrator** (the brain, acting like the thermostat of an air-conditioner), and the **effector** (brown fat, muscles—acting like the air-conditioner). If the external temperature increases above the set point, the receptor sends a message to the brain which in turn triggers an action—such as sweating, shivering and non-shivering heat production in brown fat—that reduces or increases the body temperature. This feedback system regulates the body temperature to its optimum level.

Some animals, especially those regularly exposed to cold nights and winter temperatures, can temporarily revert from endotherm to heterotherm characteristics—undergoing rapid changes in their body temperatures. This can take the form of short-term **torpor** or longer-term **hibernation**. There are few examples in Angola, but one—the White-backed Mousebird from the Cunene valley—goes into torpor at night, dropping body temperature from 40 to 26 °C, with a corresponding temporary reduction in metabolic rate and oxygen consumption. The small arid zone insectivore, Bushveld Sengi (also known as an elephant shrew because of its long nose) is also known to undergo torpor on cold nights.

Plants are more tolerant of body temperature changes, and some succulents can survive temperatures ranging from −16 to 68 °C. Plants have many adaptations to reduce heat stress, such as those cited with regard to water economy. Succulents such as *Euphorbia virosa* have thorny and deeply fluted stems, scattering radiation and thus shading half of the stem, thus minimising heat loading.

A second physical factor that strongly influences adaptations to heat is called the **boundary layer**. The boundary layer above the soil (or around a leaf) is a thin zone of calm air that influences how quickly energy (or gas) is exchanged between the soil or leaf surface and surrounding air. The gradient of heat above a sand or rock surface is very steep in the first few millimetres, as is the temperature decrease with depth below the sand surface, factors that are exploited by some desert insects and reptiles.The beetle *Stenicara phalangium* has the longest legs in any beetle and walks about as if on stilts, keeping its body above the temperature boundary layer of the desert gravel surface of their habitat. The sand dwelling Shovel-snouted Lizard has a remarkable behavioural adaptation to hot sand. It alternates lifting back and front legs, and even using its tail as a lever, to do a dance on the sand, keeping its body above the hottest levels of the boundary layer. The Shovel-snouted Lizard also has the ability to dive under the sand and burrow down to cooler levels, thus escaping the surface heat.

While endotherms have the ability to regulate their temperatures, this comes at a cost, especially for small mammals and birds, with large surface area to volume ratios. While surface coverings (fur and feathers) can moderate heat accumulation or loss, many **behavioural adaptations** make it easier to maintain a stable body temperature. Most small desert mammals, such as gerbils, are nocturnal and during the day, retreat to burrows, thus escaping the midday heat of summer or the cold of winter nights. Ground squirrels use their bushy tails as umbrellas to provide shade as they forage and feed. Springbok and Steenbok seek out shady trees, Gemsbok climb to the crest of dunes to catch cooling breezes. When grazing, many mammals such as Springbok face towards the sun to reduce the profile of their body exposed to the sun's rays, thus reducing heat absorption while simultaneously lowering their visibility to predators.

Sweating alone might dehydrate desert mammals in the absence of other heat-reducing systems. In response, a remarkable vascular anatomy and response physiology has evolved in Gemsbok and several other desert antelope to help survive the dehydrating heat of summer. The system known as **selective brain cooling**. To reduce water use, Gemsbok can stop their normal sweating behaviour on very hot days, gradually storing heat, with the body temperature rising to as much as 43 °C. If blood at this temperature were to be fed directly to the brain, death would result. A choice must be made between water-expensive sweating or temperature-threatening increases in body temperature. The delicate balance between sweating and allowing body temperature to rise is governed by the **hypothalamus**, which monitors both temperature and blood concentration, triggering responses to over-heating and dehydration.

Gemsbok and other antelope can allow their body temperatures to rise, while their brain temperature is kept within functional limits through the **carotid rete system** (Fig. 11.8). Arterial blood first passes through a network of intermingled venous and arterial blood vessels (the carotid rete) which act as a '**blood-flow radiator**', before reaching the brain. The radiator mechanism is simple and efficient. When a Gemsbok becomes hot and dehydrated, it starts to pant. The temperature of the venous blood in its nasal sinuses drops due to evaporative cooling. Hot, freshly oxygenated arterial blood from the lungs passes through the rete and is cooled by transferring heat to the colder venous blood. Through this 'counter-current heat exchange' blood passing through the carotid artery falls to 40 °C before it reaches the brain. The difference between 40 and 43 °C is the difference between life and death. It also is the difference between extreme dehydration and survival through water use efficiency, accounting for Gemsbok (and Springbok and other several other ungulates) prospering in Iona National Park even without access to open water sources.
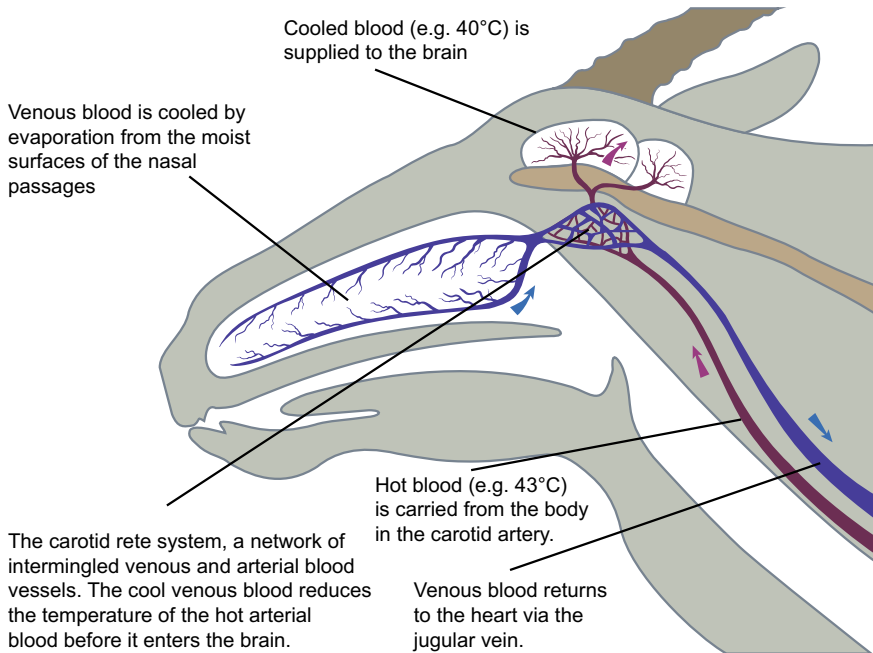
Cooled blood (e.g. 40°C) is supplied to the brain

Venous blood is cooled by evaporation from the moist surfaces of the nasal passages

The carotid rete system, a network of intermingled venous and arterial blood vessels. The cool venous blood reduces the temperature of the hot arterial blood before it enters the brain.

Hot blood (e.g. 43°C) is carried from the body in the carotid artery.

Venous blood returns to the heart via the jugular vein.

Fig. 11.8 The carotid rete system found in Gemsbok and other desert antelope. Warm arterial blood (at 43 °C) is cooled (to 40 °C) as it passes through the carotid rete before entering the brain. The animal's body temperature can rise to levels that would be lethal if the blood passing to the brain was not cooled. Redrawn from Lovegrove (1993) *The Living Deserts of Southern Africa.* Fernwood Press

11.3 Competition for Food in a Low Productivity Environment

Competition occurs when two or more individuals use a common but limited resource. The theoretical aspects of the concept are discussed in Sect. 9.5. Here a few examples from the Namib illustrate forms of competition (or avoidance of competition) relating to food, water and nutrient resources.

For an organism to survive, grow and reproduce, food is essential. In highly productive biomes, such as the tropical rain forests of Cabinda, both climatic conditions (temperature and humidity) and environmental resources (water and nutrients) are adequate for high levels of primary production. In the desert, infrequent, discrete, and unpredictable rainfall events and desiccating heat reduce primary production to very low levels. Securing a reliable food supply is an ever-present challenge. In the Namib and Kalahari, three hyaena species—Brown, Spotted and Aardwolf—coexist. Each species has defined food preferences, and interspecific competition is seldom observed. Intraspecific competion occurs along the margins of clan territories, where scents and other marking techniques are used to delimit territories. Territories are

defended by borderline disputes which normally avoid fatal confrontations, while robustly protecting access to food resources. This is an example of interference competition—where some clans are winners, others are losers.

Some competitive and facilitation processes are extremely complex. An example of interactions at different scales of interspecific competition between plant species, for water and nutrients, influenced by intraspecific competition between colonies of herbivorous termites, is described in Box 11.1. Competition for water is also a driving force, influenced by fire and herbivory, in the structuring and maintenance of savannas, as described in Chaps. 7 and 8.

More frequently observed is **habitat partitioning**, where similar food resources are divided between potentially competing species occupying distinct micro-habitats. In the Namib, four species of *Onymacris* beetles share wind-blown plant detritus and dead insect food resources, but within different habitats in dune bases, slip faces, floodplains and riverbeds -all within a small area. Habitat partitioning between the *Onymacris* species is strongly defined when resources are limited, but breaks down after unusually good rains, when resources are abundant and interspecific competition relaxes.

In all resource limited environments, the **storage** of food is a common strategy. In the Namib, both termites and ants are active food harvesters, building stores to see them through the drought periods. Research by Alan Marsh on two species of harvester ants in the Namib (Marsh, 1987) suggested that ants do not practice interference competition when resources are adequate (and stores are being built up) nor when resources are low (when it is more important to collect scarce food than to expend energy on fighting neighbours). Competitive interactions are not always the most efficient use of a species' energy.

Competition is not the only strategy for acquiring and storing food. Cooperative social behaviour ensures survival under extreme conditions, as in the case of Damara Molerats, which collect vast stores of bulbs and corms, sometimes numbering thousands of propagules. These stores are essential for burrowing molerats for whom burrowing is a difficult and expensive mechanism of food harvesting. This is especially important when food must be readily available for lactating females after giving birth to and raising pups. Furthermore, the window for successful harvesting of corms is focused on wet periods, when the energy cost of burrowing through damp sand is three times less than through dry sand. As described below, social behaviour is a key to desert survival.

11.4 Defence Mechanisms: Camouflage, Deceit, Mimicry, Spines, Poisons and Social Behaviour

Adaptations that have evolved in reponse to water scarcity, temperature extremes and limited energy budgets are pointless if an organism cannot avoid being eaten by predators before transferring its genes to the next generation. An impressive arsenal

of weaponry has been evolved in animals and plants to reduce the prospect of being preyed upon. Adaptations include avoidance strategies such as camouflage, deceit and mimicry; structures such as spines, thorns and horns; and chemical defences such as poisons to avoid or reduce predation.

Plants cannot run away from herbivores. They have to invest in defences, such as thorns, spines or poisons. A common evolutionary response to herbivory has been the development, in many families of plants, of **chemical** defences using **secondary compounds** such as alkaloids, glycosides and other toxic chemicals. These have no physiological role in plant growth other than as a defence mechanism. The objective (or more correctly, selective pressure) is to reduce herbivory, either because water is limiting (as in deserts and arid savannas) or because nutrients are limiting (as in mesic savannas). In general, plants in low fertility, dystrophic savannas use chemical defences, whereas plants in high fertility, eutrophic savannas use structural defences. Plants in low-nutrient soils are inherently slow-growing (from three- to five-fold slower in seedling growth rates) with low rates of photosynthesis and nutrient uptake. They cannot afford to lose leaf tissue through herbivory—thus they invest in chemical defences. In rich soils, growth is fast and rates of nutrient uptake and photosynthesis are high—they can afford to lose some photosynthetic tissue, rather than investing in chemical or other defence mechanisms. Thorns and spines slow down herbivory, but do not prevent it.

Secondary compounds include chemicals such as alkaloids, rotenoids, glycosides, tannins and phenols. Most are toxic, some such as strychnine can be fatal. The most common secondary compounds in plants are **tannins**. These interfere with digestive processes, reducing protein absorption. Glycosides cause heart failure. They occur in many species of geophytes, which are especially common in arid savannas and on the desert margins. Tannins seldom kill herbivores, but in mesic savannas, the high levels of tannins in the most abundant tree and shrub species accounts for them being avoided by browsers, and thus for the low biomass of mammalian herbivores in the biome. One mesic savanna geoxyle 'subterranean tree'—*Dichopetalum cymosum*—deserves mention. Known as 'gifblaar' (poison leaf) in South Africa, the leaves accumulate fluoroacetate, a cardiac poison. A mouthful is sufficient to kill an ox. Most indigenous herbivores avoid this and other geoxyles during their most toxic growth phase.

Unlike most mammals, insects have a high tolerance of secondary compounds. Some, such as the larvae of the African Plain Tiger butterfly *Danaus chrysippus* (Figs. 11.9 and 11.10) specialise in eating the highly poisonous milkweeds of the Asclepiadaceae family. Both caterpillars and adult butterflies accumulate the cardiac glycosides contained in the milkweeds, which makes them unattractive to birds and other predators. They are thus one of the commonest butterfly species in southern Africa. So successful in fact, that a non-poisonous butterfly—Common Diadem *Hypolimnus missipus*—has evolved an almost identical appearance, and they thus avoid predation while not having to expend resources on the production of secondary compounds. This form of mimicry (known as **Batesian mimicry**) is common in many insects. Another form of mimicry—**Mullerian mimicry**—is where two or more harmful species mimic one another's colouration and warning signals, thus

spreading the odds of being preyed upon. Yet another use of colour is **aposematism**, where bold colours warn potential predators to stay away from poisonous prey species. Bright red, yellow and black patterns in some bees, wasps, snakes and toads are common examples.

Camouflage and **cryptic colouration** are also very common predation-avoidance strategies in insects and in many vertebrate species. These strategies are especially common in arid environments, where colouration patterns have evolved in insects, birds, frogs, lizards, snakes and even plants that allow them to hide in plain sight. In the Namib, Peringuey's Adder will lie in the sand, hardly visible, the tip of its tail wriggling to attract an unsuspecting lizard to within striking distance. Here both camouflage and deceit work in tandem.

A perfect form of **deceit** is that of the Pearl-spotted Owl, common in both arid and moist savannas. False eye patterns on the back of its head no doubt confuse predators

Fig. 11.9 A classic example of Batesian mimicry is that of the highly poisonous southern African Plain Tiger (Fig. 11.9) which is mimicked by the female Common Diadem (Fig. 11.10)
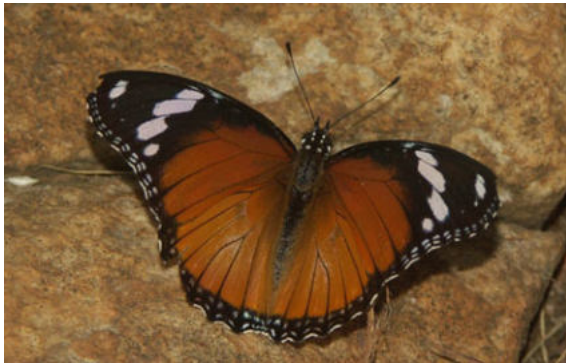

Fig. 11.10 The Common Diadem is non-poisonous, but persuades predators that it too, like the African Plain Tiger, is unpalatable. *Photo* Christopher Willis

into believing that they are being observed. **Colouration** also varies within species, and in harmony with the habitat. Leopards in arid environments such as Iona National Park are pale, while those in Bicuar National Park are richly coloured (Figs. 11.11 and 11.12).

A characteristic of arid savannas, evolved in tandem with the antelope fauna of Africa, is the **spinescent habit** of many trees and shrubs of these nutrient-rich ecosystems (Chap. 15).

Spines are not restricted to trees and shrubs. Protective **armour** is found in many animals such as pangolins, tortoises, porcupines and hedgehogs. Porcupines, because of the rich layer of fat below their skin, is a delicacy for some predators such as lion, leopard and hyaena. This is despite the needle-sharp cover of long spines, which inflict dangerous wounds on the predator. However, given the wide distribution and

Fig. 11.11 A richly coloured leopard in the miombo of Bicuar

Fig. 11.12 A pale desert form of Iona National Park. The colouration is suited to camouflage in dark, mesic (Bicuar) and dry, light (Iona) vegetation types

resilience of porcupines across southern Africa, the defence mechanism is clearly effective in the vast majority of cases.

A major theme in ecology is the role of **social behaviour**, both as a defence mechanism and in optimising reproductive output. Here we will examine the former. In a desert, a solitary existence has serious limitations. **Cooperative behaviour** can serve many of life's demands. Teamwork allows division of labour in finding, transporting, storing and defending food resources. Some insects, including bees, termites and ants, have sophisticated social organisation systems. These are called **eusocial** species—a classic example being termites—where a queen is solely responsible for reproductive success, other females being sexually repressed. Worker termites collect food, feed offspring and build nests, while heavily armed soldiers are responsible for defence. There are very few vertebrate eusocial species. One of the rare exceptions is that of the previously mentioned Damara Molerat, where highly complex social structures have been found, with queens, workers and soldiers. A lactating solitary molerat female would soon starve in its underground midden if it did not have the support of worker females.

Brown Hyaena live in cooperative clans, with some members searching for carrion within a very large home range, walking up to 50 km a night in scavenging exercises, bringing food back to the den to be shared among the clan, even by the cubs of competing males. Here the distinction needs to be made between **home range**— the area which an animal occupies throughout the annual cycle of activities—and **territory**—the more limited area within the home range that is defended for mate selection and breeding purposes. As a clan, Brown Hyaenas can defend themselves against lion or leopard attacks. Alone, the individual hyaena would have little chance of surviving an attack by a larger predator. Such behaviour requires large clans to cooperate in searching for food in arid, resource-sparse environments. In the Kalahari, for example, Spotted Hyaenas have home ranges of 380–1770 km^2, with 4–14 members per clan. In resource-rich Serengeti, clans occupy much smaller home ranges of 30–60 km^2, and the abundance of food can sustain clans of up to 80 members.

Cooperative behaviour is no less strategic in bird populations. Doves and sandgrouse have the habit of approaching water points as a large flock, swirling in to land together, reducing the chance of raptors capturing a lone individual. Sentries within the flock can keep a lookout for raptors while the other members have more time to drink. More complex sociality has evolved in the Meerkat (Suricate), a delightfully entertaining member of the mongoose family once common on the open gravel plains of Iona (Fig. 11.13). Each colony of Meerkat occupies a home range of about 6 km radius, with three or four warrens within the area, moving from one warren to the next in search of insects and scorpions. A lookout sentry keeps watch for predators such as jackals, snakes and raptors, while other members of the clan forage in the cool of morning and late afternoon. Sentries use distinct alarm calls for different levels of threat. While adults are out foraging, young females play babysitter. Such cooperative behaviour, with multiple individual responsibilities, requires a minimum number of members to sustain the community. If group size falls to too few members, the clan will die out, as has happened to many clans in Iona.

Fig. 11.13   An alert Meerkat family at their burrow in the gravel plains of Iona. Social cohesion of individuals providing sentry, baby-sitting and hunting services ensures the survival of isolated populations

Behavioural, together with morphological and physiological adaptions, form a suite of defences against desert extremes through **tolerance** or **avoidance**. While many desert organisms can tolerate high levels of heat and aridity, they survive these extremes through various avoidance mechanisms. Some are simple—short-term **retreat** such as moving into shade, or burrowing underground. Long-term responses to stress include **escape** such as the **nomadism** of many bird species. Plants cannot move from place to place, but escape extended dry periods in the form of dormant seeds or as underground bulbs. This is particularly the case in annual species, which are very short lived, sometimes requiring only a few weeks following a rainfall event of more than 10 mm to grow, flower and set seed (Henschel et al., 2005). The mass spring flower displays in the southern Namib and especially in Namaqualand, South Africa, are world famous for their beauty.

11.5   Reproduction and Survival in Desert Environments

The success of reproduction of animals and plants is the most important, risky and expensive investment in an organism's life. In stable, predictable and productive environments such as tropical rain forests, emphasis might be given by plants to investing in complex co-evolved relationships with pollinators and other organisms to ensure successful fertilization in highly competitive, species-rich ecosystems. In deserts the challenges, as we have seen, are more physical—heat and aridity, unpredictability of rainfall timing and quantity.

Timing is key. For some groups of animals, the timing of reproduction, to ensure that births occur when resources are at their most accessible, is controlled by photoperiod (day length). **Photoperiod** is monitored by the eye, sending signals via the optic

nerve to the pineal gland in the brain which triggers the release of the hormone **melatonin**. Melatonin influences the activity and growth of the sexual organs—the testes and ova. Daylength thus regulates breeding cycles.

Secondary time-givers include rainfall events and the quality of food. Rainfall at any time of the year can trigger breeding activity in the Sociable Weaver of the Kalahari, which can have as many as four broods during infrequent episodes of high rainfall. Large mammals, with long gestation periods, are less likely to be able to respond to unpredictable rainfall events and thus they rely on photoperiod. Besides triggering reproductive activity in mammals, photoperiod also signals dormancy and migration and, in plants, flowering and germination. In some habitats, breeding seasons are more limited, with large numbers of Impala or Wildebeest calves being dropped within a few weeks, thus reducing predation pressure by essentially 'flooding the market'. Other species, such as Springbok, spread their calving over longer periods, ensuring that at least some are born during a time of sufficient forage. However, timing is but one of many factors influencing the success of the reproductive act and the patterns of reproductive optimisation for different habitats, functional suites or taxonomic groups. These various life history patterns have been classified in many ways, the most widely used being that of *r*- and *K*-selection strategies, as discussed in Sect. 9.4.

Box 11.1 The Enigmatic Fairy Circles of the Namib Desert

It is appropriate to conclude Part lll of this book on ecological concepts and processes with an account of an ecological phenomenon that has challenged scientific explanation for many decades—the '**fairy circles**' of the Namib Desert. The fairy circles, nowhere more abundant than in Angola, have several attributes that deserve attention:

- The circles stimulate interest because of their regular pattern over a latitudinal distance of more than 1800 km of arid, hostile environments.
- They have challenged ecologists to draw on a wide range of ecological concepts—at organismic, population, community and biome levels—to help explain the phenomenon.
- They have also demonstrated the scientific method in practice—of proposing hypotheses, collecting detailed data with which to test ideas, accepting or rejecting alternative explanations, and finally seeking a convincing understanding of complex natural phenomena.

The fairy circles are found as a narrow belt within the arid grasslands that lie along the eastern margin of the hyper-desert and below the foothills of the continental escarpment (Fig. 11.14). Isolated pockets of fairy circles are found from the Richtersveld of South Africa to Carunjamba in Angola, within a narrow zone of 80–150 mm mean annual rainfall. From the air, as shown in satellite images, the fairy circles look like polka-dot spots across the landscape,

with each patch having an average of six neighbours in a regular hexagonal pattern. On the ground, the bare patches average about 5 m in diameter, but range from 2 to 55 m diameter, with from 5 to 50 patches per ha (Figs. 11.15, 11.16 and 11.17).
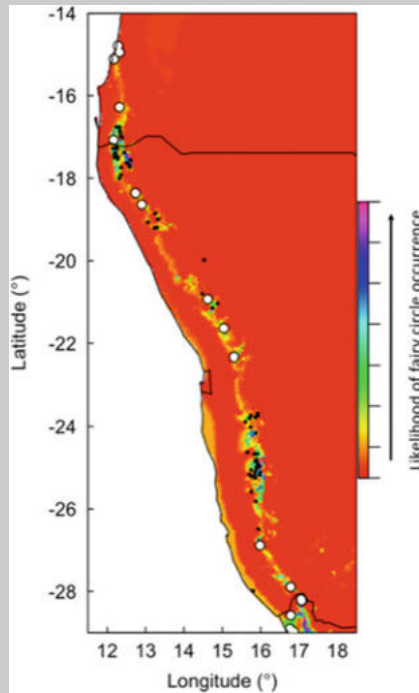

Fig. 11.14 Observed distribution of fairy circles (black and white dots) and modelled predicted locations. From Cramer and Barger (2013) *PLoS ONE*, 8, e70876

Fig. 11.15 Google Earth (Landsat/Copernicus) Satellite image of Iona National Park. The northern limits of the Cunene and Curoca Sand Seas are clearly defined, as is the sand spit of Baía dos Tigres. This image covers 60 km west to east and is centered at 16°49′20″S; 12°51′14″ E

Fig. 11.16 Stable transverse dunes in central Iona (Vale dos Rinos) pock-marked by hundreds of 'fairy circles'. The image covers 1 km west to east. This Google Earth (Landsat/Copernicus) image is centered at 17°00′55″ S; 12°17′55 E

Fig. 11.17 Fairy Circles' on the arid grasslands of Iona National Park. Left: Two opposing dune systems, older longitudinal and younger latitudinal, on the intermontane basin of Vale dos Rinos. Serra Ongamule in background

Within a grassland **matrix** of short (20 cm) desert grasses (*Stipagrostis uniplumis* and *S. hirtigluma*) the bare **circular patches** are fringed by taller (50 cm) grasses (*Stipagrostis geissii, S. ciliata*) which form a distinct, narrow **perennial belt**. The bare patches are slightly deflated by desert winds, maintaining a shallow basin profile with a raised margin due to accumulation of sand against the perennial belt. The circles increase in diameter and decrease in density from south to north across their 1800 km latitudinal range. The circles are dynamic, appearing and disappearing over decades to centuries. A unique feature of the pattern of these regular bare patches in the arid grasslands of deep sands is that the phenomenon is known only from the Namib Desert and from an isolated area in Western Australia; nowhere else on the planet (Fig. 11.18).

Fig. 11.18 Bare patches of typical 'Fairy Circles', Iona National Park, Namibe province

Naturalists are fascinated by patterns in nature, especially non-random or **over-dispersed** (evenly spaced/ non-random) patterns. For the past half century researchers have speculated on the origin of the fairy circles. Many popular myths explaining the origin of the circles were told to visitors to Iona National Park during colonial days These anecdotal accounts related that the bare circles were sites where zebras rolled on the ground to free themselves of ticks, or that they were caused by a shower of meteorites, or that growth-inhibiting radioactive compounds killed off seedlings, or that the circles mark the sites of fossil termitaria (Huntley, 2017). Such innocent speculations have been succeeded by a surge of sophisticated research over the past two decades, leading to a heated debate conducted in leading journals of science. Several hypotheses have stimulated the discussion and deserve consideration:

- The bare patches result from the activity of **sand termites** (Juergens, 2013, Juergens et al., 2015);
- Competition between grass species for water result in patterns of **self-organisation** (Cramer & Barger, 2013; Getzin et al., 2015).
- Latex and other exudates from species of *Euphorbia* release **hydrophobic/allelopathic** chemicals which suppress or prevent grass germination and growth on the sites where dead *Euphorbia* plants decompose.
- The above hypotheses are not mutually exclusive (Pringle & Tarnita, 2017; Tarnita et al., 2017).

Sand Termite Hypothesis

Since the 1980s Norbert Juergens of the University of Hamburg has conducted studies across the full length of the fairy circle belt. He has assembled detailed and long-term data (Juergens, 2013; Juergens et al., 2020) as evidence that two species of herbivorous **sand termites** *Psammotermes allocerus* and *Microhodotermes* sp.nov. are the driving force of what he describes as fairy circle ecosystems. Juergens et al., (2020) found that the more widespread *Psammotermes* is responsible for the smaller, more densely patterned fairy circles that occur from southern Namibia to northeast Iona National Park, while *Microhodotermes* creates larger, less dense fairy circles from Iona northwards to Carunjamba. The process proposed by Juergens, specifically for *Psammotermes*, is as follows.

After an infrequent rain event, the termites remove short-lived annual grasses from an initial patch within the grassland matrix, creating a grass-free gap which allows more effective water penetration through the large pores of the sandy soil. The absence of grasses results in reduced evapotranspiration from the developing bare patch. Furthermore, the concave surface of the gap concentrates moisture from fog precipitation or during rare rainfall events. The moist sand, at a depth below 30 cm is supplemented by later rains, and

builds a 'cistern'—a reservoir sufficient to maintain the termite population in their underground galleries and also the tall perennial grasses of the margin of the bare patch. The termites maintain the bare patch, removing potential competition for resources from grass invasion. This activity ensures the maintenance of the 'water trap' created by the fairy circle. The perennial grass belt demarcating the perimeter of the fairy circle provides a food store for the termites during droughts, when the grasses of the wider matrix might be removed by herbivores, decomposition or wind erosion. In Iona National Park, the termite activity, demonstrated by the sheetings (plastering) of grass stalks of the fringing *Stipagrostis geissii* perimeter, and small dumps of sand at the termite colony entrances, are common sights, lending support to the termite hypothesis.

The result of this classic example of **ecological engineering** is a mini-oasis that persists through droughts and attracts many species of invertebrates, plus vertebrates such as sand lizards, geckos, aardvarks, gerbils, golden moles, goshawks, Bat-eared Foxes and Black-backed Jackals. Juergens (2013) documents a biodiversity two orders of magnitude greater in the patches than that of the short-grass matrix. Juergens (2013) describes a functional micro-ecosystem, with its own hydrology, microclimate, microorganisms and plant and animal diversity centred on the fairy rings. It is a perennial ecosystem in an ephemeral desert. The finding by Juergens et al. (2020), that two similar but distinctive fairy circle ecosystems in the Namib result from the activities of two termite families (Rhinotermitidae and Hodotermitidae), provides both a fascinating example of parapatric convergent evolution and strong support for the termite-driven origin of the phenomenon.

Self-organisation Hypothesis

A second hypothesis was tested by researchers from the universities of Cape Town and Colorado. Cramer and Barger (2013) proposed that fairy circles are emergent, **self-organising vegetation patterns** resulting from belowground resource competition and facilitation between grasses. While recognising the possible subsidiary roles of termites and ants, they found that local-scale availability of total nitrogen, soil moisture and rainfall resources are inversely correlated with the size and density of fairy circles. They describe the formation of bare circles as the result of initial gaps forming within individual clonal grasses, such as *Stipagrostis ciliata*, with facilitative feedback from larger, deep-rooted plants with access to deeper water resources and runoff. They cite theoretical models in support of their predictions, based on competition for water between grass clumps and neighbouring fairy circles, as the causal mechanism for the bare patches and their **over-dispersed** (evenly spaced/non-random) distribution pattern. Once a gap is established, it results in the formation of a water and nutrient reservoir, supporting the growth of larger grass species on the periphery, as described by Juergens (2013). They conclude that

lower soil carbon and nitrogen and moisture field capacities of fairy circle soils compared with matrix soils are emergent properties of the circles, rather than causal factors. The maintenance of the bare circles might be facilitated by wind blowing grass propagules off the barren circles, with both termites and ants possibly contributing to grass mortality in the circles. From Cramer & Barger's field studies, they propose that competition between grasses for water and nutrients, and positive facilitation feedbacks, not termite herbivory, are the drivers of fairy circle formation and maintenance.

Further studies were undertaken by Stephan Getzin from the Helmholtz Centre in Leipzig, Germany, based remote sensing, spatial pattern analysis and vegetation modeling (Getzin et al., 2015). Using mathematical models and field observations they describe regular, large-scale self-organising vegetation patterns driven by small-scale ecological feedbacks that result from competition for scarce soil water, supporting Cramer & Barger's hypothesis.

Euphorbia Chemical Release Hypothesis

In another detailed study, combining chemical, phytochemical, historical records and GIS spatial patterning evidence, Marion Meyer and colleagues from Pretoria University (Meyer et al., 2020) propose that **hydrophobicity** (water-repellency) of latex compounds from the decomposition of *Euphorbia* species (*E. damarana, E. gummifera* and possibly *E. gregaria*) causes the sand in the circles to repel any water falling on the site of dead euphorbias. The circles are thus much drier than the surrounding matrix of grassland. Seeds that do germinate in the circles do not survive for very long. Further, the hydrophobic properties of the affected fairy circles might concentrate water at their periphery, supporting robust growth of grasses in the perennial belt. The study also reported phytotoxic, allelopathic and antibacterial activity resulting from the chemicals released by the *Euphorbia* plants. What the study did not explain was the presence of fairy circles in sites where dense populations of *Euphorbia* species are absent or rare in typical fairy circle habitats, such as the sandy plains of the Vale dos Rinos, Iona National Park. However, the absence of euphorbia communities under the present climatic conditions does not preclude the possibility that the distribution of euphorbias might have expanded and contracted with changes in the patterns of rainfall during the Pleistocene and Holocene. Today's euphorbia distribution might be the consequence of shifts in rainfall patterns, with sites previously occupied being reflected in current fairy circles, maintained by hydrophobicity 'scars' in the sands, as ecological fingerprints of the past. Not surprisingly, in the ongoing debate over the origins of fairy circles, Getzin et al. (2021) present a series of arguments contesting the hydrophobicity theory.

Integrative Systems Hypothesis

Following active debate on the termite and self-organising hypotheses, Robert Pringle and Corina Tarnita of Princeton University, USA (Pringle & Tarnita, 2017; Tarnita et al., 2017), have found that the competing proposals are valid; that intraspecific competition between territorial animals (sand termites) and scale-dependent feedbacks through facilitation and competition for resources (desert plants) can result in regular patterns in nature such as the fairy circles. Furthermore, they found multi-scale patterning in the Namib grasslands that they suggest can only be explained by integrating both mechanisms (termite foraging and plant competition), thus providing a unifying hypothesis that accounts both for pattern and for emergent properties such as ecosystem resilience to drought events.

Studies on the origin of the fairy circles provides insights into the development of ecological knowledge, beyond the scope of this book, but very instructive to the student. Detailed field biological studies, ecological modelling, and the matching of theory to observations, followed by criticisms and rebuttals, provide perspectives on what at first sight appears as a simple pattern of bare patches in homogeneous grassland. The enigmatic fairy circles of the Namib provide an elegant model of the scientific method in action and of the role of curiosity-driven, rather than what might be regarded as more socially relevant, science.

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