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Animals at the extremes: The desert environment

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Introduction

This course is the first in a series of three on **Animals at the extreme**. It is concerned with the integration of behaviour anatomy, physiology and biochemistry in diverse vertebrates that live in deserts. Once you have completed this course, you will be all the more able to appreciate the linked courses that follow, **Animals at the extreme: hibernation and torpor** and **Animals at the extreme: the polar environment**. These courses build on and develop some of the science you will study here.

This OpenLearn course provides a sample of Level 3 study in Science.

Learning Outcomes

After studying this course, you should be able to:

- define and use, or recognise definitions and applications of, each of the bold terms
- provide examples that show there is a continuum of desert climates and environments that link to diversity of flora and fauna
- explain, with examples, the thermoregulatory strategies of evaders, evaporators and endurers, and interpret relevant data
- describe the importance of integration of behaviour, anatomy, physiology and biochemistry in the study of animals that live in deserts
- explain physiological mechanisms of water conservation and cooling in named evaders, evaporators and endurers, and interpret relevant data.

1 The desert climate: An introduction

If you have visited a desert you will have noticed the sparse plant cover, or in certain sandy deserts, the almost complete absence of plant life. The low productivity of deserts derives from their defining feature, which is aridity. Scarcity of water restricts the diversity and amount of plant cover, and in turn the diversity and abundance of animals. However, if you were visiting one of the American deserts after rains, you would be rewarded by the sight of the desert ‘in bloom’, as vast swathes of annual plants such as the Mojave aster (*Xylorhiza tortifolia*) and sand verbena (*Abronia villosa*) flower simultaneously. You might catch sight of insects such as beetles and locusts, and vertebrates including lizards and occasionally mammalian herbivores, such as gazelle, in African deserts and oryx in the Arabian desert.

Hot deserts located 15°–25° north and south of the Equator have daytime sunshine all year round (Figure 1). The persistent descending air and stable high pressures create the hot climate. While daytime temperatures can be as high as 45°C, night-time temperatures may be close to freezing as heat is lost by radiation into the clear night skies.

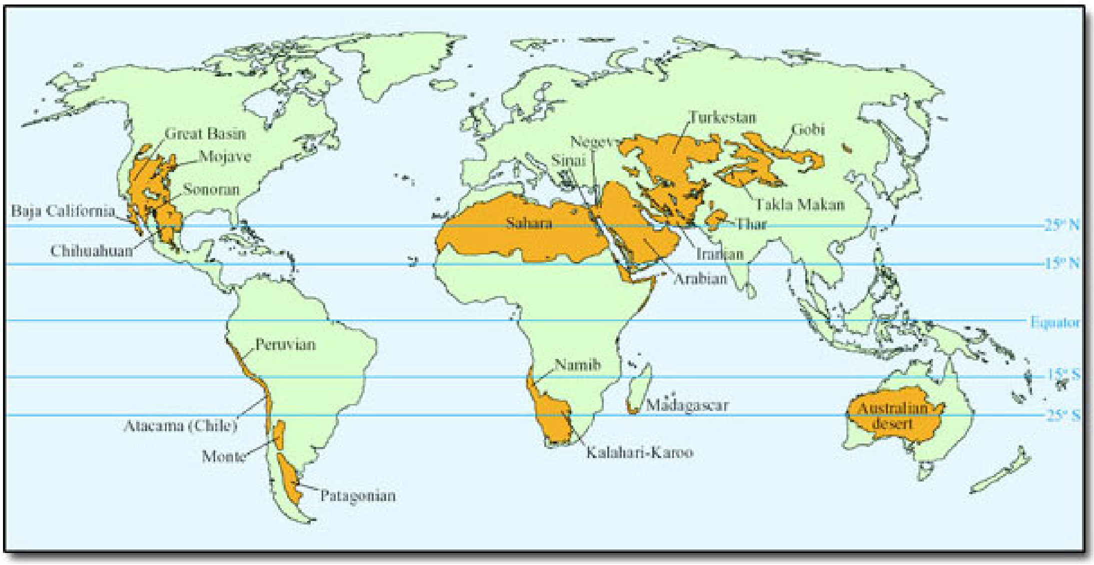

Figure 1 Locations of deserts worldwide showing the broad latitudinal belts north and south of the Equator

Willmer et al. (2000) The occurrence of deserts on a worldwide basis …, *Environmental Physiology of Animals*, Chapter 14. Blackwell Science Limited

Willmer et al. (2000) The occurrence of deserts on a worldwide basis …, *Environmental Physiology of Animals*, Chapter 14. Blackwell Science Limited

Aridity of deserts has three main causes. The deserts in parts of North and South America are arid because they are located on the leeward side of mountain ranges in rain shadow. Rain falls as moisture-laden air rises up the mountains, so that the air is dry by the time it reaches the leeward side. The Gobi and Turkestan deserts lie in the centre of a large continent and their lack of rainfall is because they are a long distance from the sea. The Sahara (Figure 2) and Arabian deserts are arid because of persistent large high-pressure masses of dry air that prevent penetration of rain-bearing storm systems. A popular concept of deserts is based on the extreme Sahara, where huge areas of sand dunes support little, if any, plant growth. Certain animals such as camels (*Camelus* spp.; Figure 3), Dorcas gazelle (*Gazella dorcas*; Figure 4) and oryx (Figure 5) that survive there by browsing on the sparse plant life and drinking very little or no free water, are regarded as typical desert species.

Figure 2 The Sahara desert near Erfoud, Morocco

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Figure 3 A dromedary camel (*Camelus dromedarius*)

Science Photo Library

Figure 4 Dorcas gazelle (*Gazella dorcas*)

David Robinson, The Open University

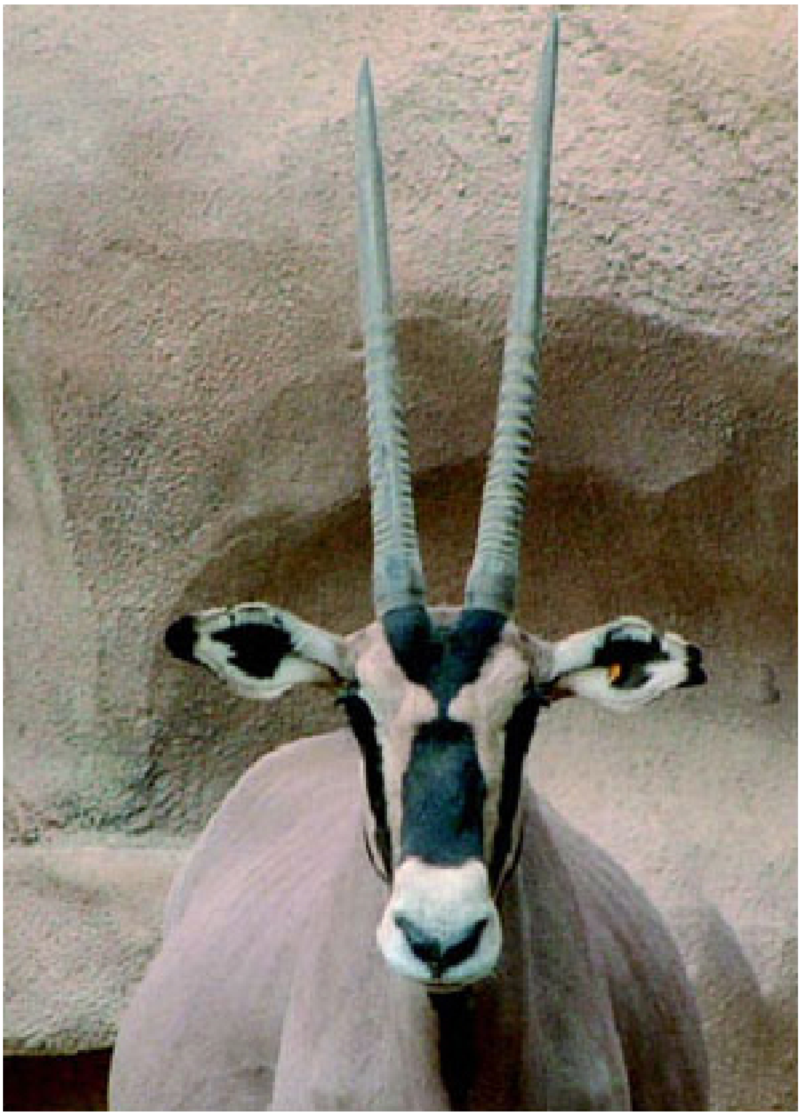

Figure 5 Oryx

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In fact the picture is much more complex; the environment of each desert is unique, and depends on the interaction between T_a, precipitation, relative humidity and wind. A useful classification is that of Meigs (1953), who defined deserts according to aridity (Table 1). The aridity of a desert is determined not just by precipitation but also by the evaporation and transpiration of plants. In order to simplify classification of arid and semi-arid areas, various types of aridity index have been devised. De Martonne's aridity index has been used widely and is calculated from the formula:

$$I_a = \frac{P}{T+10} \quad (1)$$

I_a = aridity index

P = mean annual precipitation/mm

T = mean annual temperature/°C

Note that values for average precipitation can be misleading because in arid deserts, especially hyper-arid desert, there are many years that have no rainfall at all. Certain coastal deserts such as the coastal strip of the Arabian Peninsula obtain part of their annual precipitation from thick fog, caused by cold sea breezes that increase humidity sharply. Subdivisions of aridity index are roughly the same as those for average rainfall.

Table 1 Definition of deserts according to aridity (Meigs, 1953 and UNEP, 1992).

Rainfall/mm yr^{-1}	Aridity index	Aridity	Examples
< 25	< 5	Hyper-arid	Namib; Arabian
25–200	5–20	Arid	Mojave
200–500	20–50	Semi-arid	Parts of Sonoran

All deserts have a wide range of T_a, but mean annual temperatures vary from desert to desert. Deserts can be defined as hot, mild, cool or cold (Table 2), but the reality is a continuum of desert climates rather than a set of desert climates each with a well-defined rainfall and T_a range.

Table 2 Definition of deserts according to mean T_a (adapted from Meigs, 1953).

Climate	% of deserts	Examples	Mean T_a coldest month/°C	Mean T_a warmest month/°C
Hot	43	Central Sahara; central Australian	10–30	> 30
Mild	18	Kalahari-Karoo, Chihuahuan	10–20	10–30
Cool	15	Mojave, Namib	0–10	10–30
Cold	24	Gobi	< 0	10–30

Deserts may have seasonal climates, with winters being much colder than the summers. The Sonoran desert covers about 260 000 km^2 and spans the western part of the Mexican state of Sonora, southwest Arizona, southeast California and Baja California. Average rainfall is 120–300 mm yr^{-1}, with the rain falling in two seasons. Storms from the North Pacific bring gentle rain from December to March, and surges of wet tropical air bring in rain storms from May to September. Winter temperatures are cool, averaging 13°C, and summers are extremely hot, reaching 40°C on average, but peaking at 50°C. Ambient temperatures can vary by as much as 40°C in a day. It is also important to appreciate that there are variations in climate, topography and vegetation within a desert. The Lower Colorado River Valley region of the Sonoran desert (Figure 6) is the driest hottest area, where annual rainfall may be < 50 mm and summer daytime temperature 50°C, with surface temperatures reaching 82°C; according to Meigs' classification this desert would be classed as arid hot. Vegetation there consists of drought-tolerant shrubs and succulent cacti; following winter rainfall there is rapid growth of annual plants, which cover the ground in a mass of blooms. Within the Lower Colorado River Valley there is a large area of sand dunes forming a huge sand sea. In contrast, the Arizona Upland region has an annual rainfall of 70–300 mm, making it an arid or semi-arid desert according to Meigs. There is abundant vegetation including trees such as ironwood, blue paloverde and cat claw acacia. Cacti include 12 species of cholla (*Opuntia* spp.) and also saguara cactus (Figure 7). Scrub plants include desert saltbush and creosote bush. Winter annuals, e.g. California poppies, bloom in profusion after rain.

Figure 6 The Lower Colorado River Valley region of the Sonoran desert

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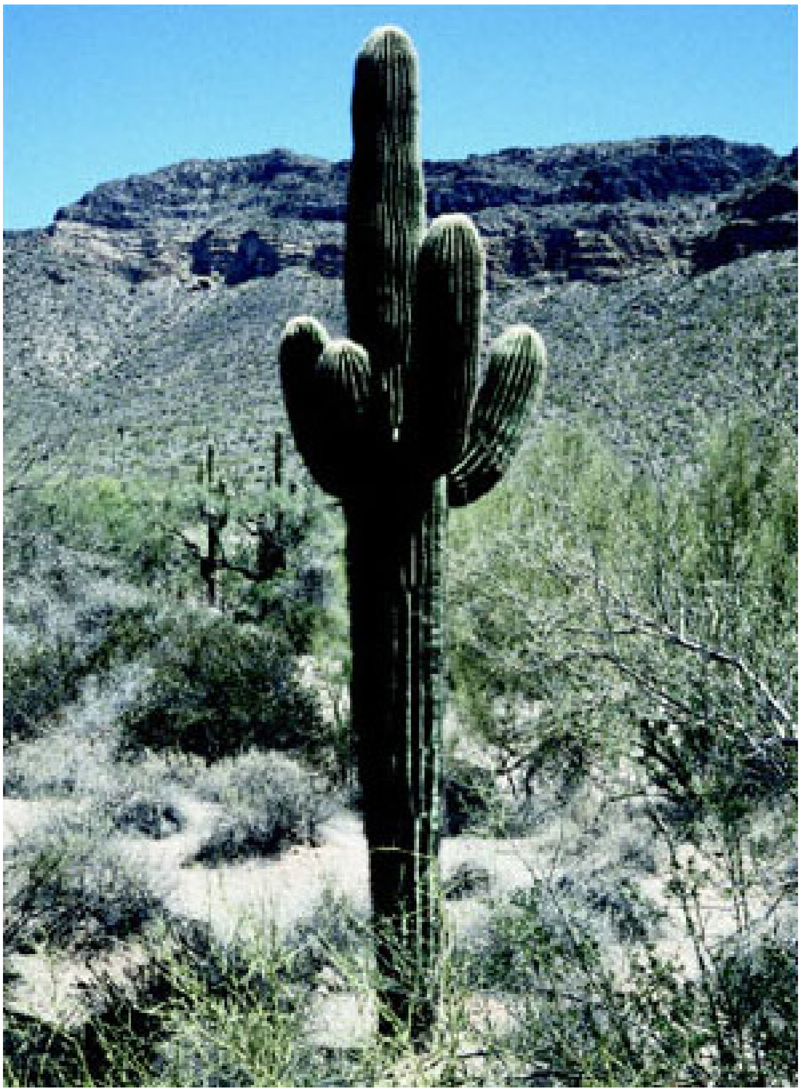

Figure 7 Saguara cactus in the Sonoran desert

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The Mojave desert spans the transition between the Sonoran and Great Basin deserts and extends throughout southeastern California, and parts of Nevada, Arizona and Utah, occupying about 100 000 km^2. Summers are hot and windy, but during the winter, temperatures can dip to below freezing. The Mojave desert is arid, with only about 130 mm rainfall per year in a winter rainy season, but the rains fail in some years. The plant life in the Mojave desert comprises *Yucca* species, including the joshua tree, big sage brush, bladder sage and creosote bush and at least 200 other endemic species.

Despite the variations in the environment of different deserts, it is correct to say that all desert animals have to cope with water shortage, and animals living in hot deserts cope with extremely high daytime T_a. Physiological problems linked to high T_a are those associated with hyperthermia. Mammals and birds have an optimal core T_b of around 38°C, and many species cannot tolerate increases > 2°C or so. The denaturation of crucial proteins, such as enzymes, begins at around 40–42°C, so hyperthermia also creates physiological problems for ectotherms. Daytime temperatures in desert environments can be much higher than the optimal T_b, e.g. up to 56°C in Death Valley, California. Homeotherms subjected to heat stress use a suite of physiological mechanisms for cooling the body, which we will explore in later sections. Evaporative cooling is the most effective way for an animal to lower T_b, yet if water is in short supply, dehydration is a serious problem, and the use of evaporative cooling is restricted. Behavioural mechanisms play an important role in cooling the body, both in desert ectotherms such as lizards, snakes and amphibians, and endotherms, such as birds and mammals.

Summary of Section 1

Despite deserts being diverse, they all have aridity in common as their salient climatic feature. Classification systems attempt to group deserts in terms of their aridity or mean annual temperatures. Major physiological problems for animals living in deserts include hyperthermia due to intense daytime solar radiation, and also hypothermia at night when desert T_b can be below freezing. The shortage or lack of drinking water in deserts means that evaporative cooling cannot be used freely for physiological thermoregulation.

2 Environments and populations

2.1 Introduction

The unique climate and topography of each desert links to the unique and characteristic flora and fauna found there. From the brief description of deserts provided in Section 1, you can appreciate that a desert provides a variety of niches for animals and plants. The term ‘niche’ applied to animals describes its role in a particular environment, and includes a number of characteristics such as habitat range, how the animal feeds, its diet, its environmental requirements and also its predators. So a niche is effectively an animal's particular lifestyle within an ecosystem, and encompasses how it interacts with other organisms and the physical environment within that ecosystem. In desert ecosystems, insectivorous, herbivorous and seed-eating niches are occupied by small animals, including arthropods, lizards, small birds, rodents, squirrels and shrews. Medium and large-sized animals such as hares, gazelle, camels and ostrich occupy grazing and browsing niches. Predators include foxes, e.g. kit fox (*Vulpes macrotis*) and cats, e.g. cougar (*Puma concolor*) in the deserts of the southern USA and Mexico, and Rüppell's fox (*Vulpes rueppelli*) in the Arabian desert. Desert vertebrates make use of a variety of microenvironments and their associated microclimates, small-scale areas in which the climate is different from that of the habitat as a whole. For example, in a desert ecosystem, a cavity beneath a rock, a microenvironment, would have a lower T_a than the surface and hence a different microclimate. A hyper-arid sandy desert, such as the Arabian desert, has a relatively low variety of microenvironments and associated microclimates available for vertebrates. Nevertheless, the sand at a few centimetres depth is significantly cooler than at the surface, and provides a relatively cool microenvironment for animals. In contrast, American deserts such as the Sonoran have a diverse range of microenvironments, and contain a richer diversity of vertebrate species.

Although our discussion here is restricted to vertebrates, you should be aware that many invertebrates, particularly insects, inhabit desert environments, and they provide an important food supply for many desert birds and mammals.

2.2 How animals interact with the environment is affected by their body size

Willmer et al. (2000) classify desert animals in terms of the range of body sizes and the rate of evaporation (Figure 8).

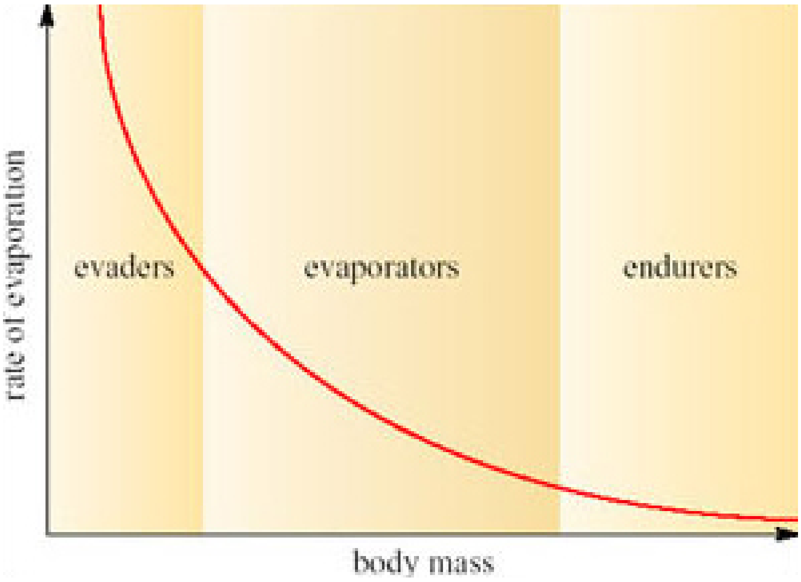

Figure 8 Classification of desert animals based on body size and rate of evaporation

Willmer, P., Stone, G. and Johnston, I. (2000) *Environmental Physiology of Animals*. Blackwell Science Limited

Willmer, P., Stone, G. and Johnston, I. (2000) *Environmental Physiology of Animals*. Blackwell Science Limited

The logic of this classification can be appreciated by the following exercise. If you represent a small animal by a cube, and then make a larger scale model of it twice natural size, the linear dimensions of the larger animal would all be twice as large (Figure 9).

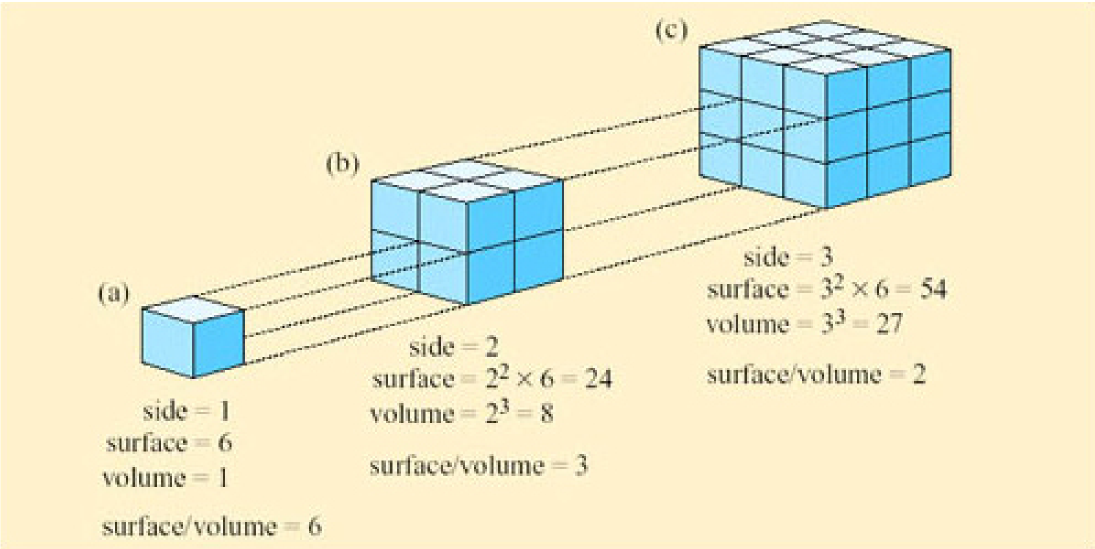

Figure 9 The linear dimensions, surface areas and volumes of three different-sized cubes are compared here to show how surface area: volume ratio decreases as the linear dimensions increase

However, the surface area of the model would not be increased by a factor of 2, nor would the volume, as can be seen by comparing Figure 9a and b. If the linear dimensions double; the surface area increases by a factor of 4 (2^2) and the volume by a factor of 8 (2^3). So the ratio of surface area to volume is lower in a large animal than a smaller one. Since heat is transferred at the surface, a small animal has greater potential for rapidly gaining and losing heat than a larger one because of its relatively large surface area. A smaller animal also has greater relative potential for evaporative water loss through its greater area of skin.

However, animals are not cube-shaped, and as you will learn in Section 2.5, certain desert species have features that can increase their surface area relative to their volume.

2.3 Behavioural strategies of evaders

Small animals, classified as evaders, include desert amphibians and reptiles, and also mammals, rodents and insectivores. The term ‘evaders’ refers to the animals’ behaviour, which helps to prevent overheating of the body on hot sunny days, 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 and shade cast by plants, for behavioural thermoregulation. Evaders also prevent excessive cooling of the body by behaviour, retreating to shelter when T_a plummets at night.

The ultimate evaders are desert frogs such as *Cyclorana* spp. (Figure 10) and *Neobatrachus* spp. (Figure 11) from Australia, which spend most of the year in aestivation, inside a burrow. Aestivation is a special kind of dormancy, which enables animals to survive lack of water and high T_a during a hot dry season. During the short rainy season, desert frogs accumulate water in the bladder, where it remains during aestivation. A famous example, *Cyclorana platycephala* (Figure 10), is known as the water-holding frog; aboriginal people used to dig up the aestivating frogs and squeeze them, in order to collect and drink the water.

Figure 10 The water-holding frog (*Cyclorana platycephala*)

Robinson, M. (1999) Water-holding frog …, *A Field Guide to Frogs of Australia*, p. 76. New Holland Publishers

Robinson, M. (1999) Water-holding frog …, *A Field Guide to Frogs of Australia*, p. 76. New Holland Publishers

Figure 11 Painted burrowing frog (*Neobatrachus sudelli*)

Robinson, M. (1999) Family Myobatrachidae, *A Field Guide to Frogs of Australia*. New Holland Publishers

Robinson, M. (1999) Family Myobatrachidae, *A Field Guide to Frogs of Australia*. New Holland Publishers

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 keratinised, and prevents loss of water from the frog's body during the 9–10 months of aestivation. At the start of the rainy season, heavy rain with consequent seepage of water into the frogs' burrows, stimulates the frogs to emerge. Breeding and feeding occur during the short wet season.

Reptiles with a scaly keratinised skin are not so prone to evaporative water loss as amphibians, and are the vertebrates that you are most likely to see on a visit to a desert. Reptiles are ectotherms and rely on solar radiation for warming the body, and maintaining high T_b during the day. Desert reptiles have no problem in gaining heat for maintaining T_b at a high level on hot sunny days (Figure 12).

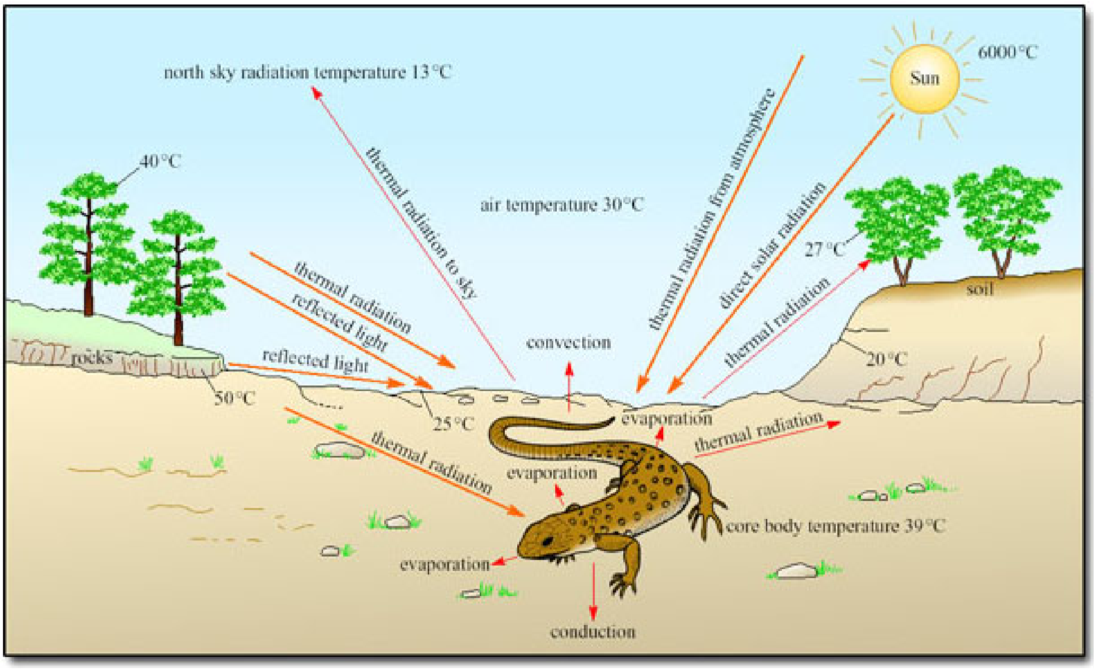

Figure 12 Heat exchange with the environment in a terrestrial reptile on a hot sunny day

Activity 1

What are the sources of energy gain and routes of heat loss for the lizard?

Answer

The lizard gains heat energy via thermal radiation from the Sun, the atmosphere and the ground. Heat energy is lost via conduction from the body to the ground, by evaporative water loss, convection and thermal radiation to the sky.

On a hot sunny day, more heat is gained than lost, and it is important for a desert reptile to avoid overheating. It is equally important to reduce loss of body heat when T_a plummets at night or during the winter.

During the day, reptiles may move between warm and cool areas in order to maintain T_b. This movement between warm and cool areas for maintaining eccritic temperature is called **shuttling**. Those species that maintain high stable T_b when environmental conditions allow by adopting heliothermic strategies, are called **thermal specialists**. In contrast, there are some species, known as **thermal generalists**, which allow their T_b to fluctuate and decline, even when they could shuttle between sun and shade to maintain high stable T_b during the day, or use their burrow at night to prevent cooling of T_b to the outside T_a. Bedriagai's skink (*Chalcides bedriagai;* Figure 13) is a thermal generalist, preferring to spend a lot of time hiding under rocks rather than basking in the sun.

Figure 13 Bedriagai's skink (*Chalcides bedriagai*)

Dr Peter Davies

The side-blotched lizard (*Uta stansburiana*; Figure 14), found in the Sonoran desert, is a typical thermal specialist. It is a small species, only 4–6 cm long when full grown.

Figure 14 The side-blotched lizard (*Uta stansburiana*)

Wardene Weisser/Ardea

In the morning, *Uta* warms by basking, initially orientating itself at right angles to the Sun's rays and flattening the body against the substratum for maximum exposure to solar radiation. When warmed *Uta* turns the body so that it faces the Sun while resting. *Uta* maintains T_b around 36–38°C. Active foraging for insects, scorpions and spiders may overheat the body, and for cooling off, especially around noon, *Uta* moves to the shade of rocks and scrubby bushes. Shuttling in this way enables this species to stay active during the day for most of the year except in areas where winter temperatures dip to freezing.

A few desert reptiles are nocturnal; the Moorish gecko (*Tarentola mauretanica*; Figure 15), is found in arid regions in North Africa (also in Spain, France and Greece, so it is not restricted to deserts).

Figure 15 The Moorish gecko (*Tarentola mauretanica*)

Dr Peter Davies

Tarentola is most active for a few hours after sunset. During the night, its T_b is as low as 18°C, and can fluctuate by up to 11°C. Recall that lizards that tolerate wide fluctuations in T_b, even when they could use features of the environment to maintain a steady T_b, are known as thermal generalists. The Moorish gecko is a thermal generalist at night, when it is active rather than resting in its burrow. During the early morning the Moorish gecko basks in the sunlight and its skin darkens until almost black. At night the gecko is very pale.

Activity 2

What advantages do the changes in skin colour give?

Answer

Dark colours absorb and radiate heat better than light colours. At night a light colour should reduce heat loss by radiation, and there is not much heat available to absorb. During the day, dark skin promotes absorption of solar heat. Although radiation to the atmosphere by the dark skin is also promoted, the energy so lost is of little significance compared to the large amount of solar heat absorbed.

The advantage to the gecko of warming up in the morning is uncertain, but it is possible that a physiological process such as digestion of the food eaten during the night requires a higher T_b than the gecko can maintain at night.

The ability of the gecko to vary skin colour shows that behavioural thermoregulation in reptiles is supplemented by physiological mechanisms, which we will explore further in Section 3.4.

Sheltering in the available shade in the desert, or being active at night, are simple strategies for keeping T_b below lethal levels. In sandy desert areas, the sand itself plays an important role in behavioural thermoregulatory strategies. The Mojave fringe-toed lizard (*Uma scoparia*) (Figure 16) is restricted to fine, wind-blown sand, e.g. in dunes, dry lake beds and desert scrub in the Mojave desert. Burrows in sand collapse immediately or soon after the animal has moved on, so animals buried in sand rely on air trapped between sand particles for breathing. *Uma* is a 'sand-swimmer' and its dorsoventrally flattened body and shovel-shaped head facilitate movement through the sand, which is especially important when escaping from predators such as snakes and badgers.

Figure 16 The Mojave fringe-toed lizard (*Uma scoparia*)

Brad Alexander

The eyelids are protected from sand by large eyelid fringe scales. The digits have large lamellar fringes, elongated scales, especially long on the hind feet, which enable the lizards to run at speed on the sand surface. *Uma* grows up to about 110 mm in length, and its activity pattern is diurnal, varying according to ambient temperature. In March and April *Uma* is active for short periods because of the low spring temperatures in the Mojave. In summer, from May to September, the lizards are active during mornings and late afternoons, feeding on insects and plants. Sand-swimming lizards are also found in the Namib desert and include the wedge-snouted sand lizard (*Meroles cuneirostris*).

The data in Figure 17 were collected from a sand dune slope in the Namib desert.

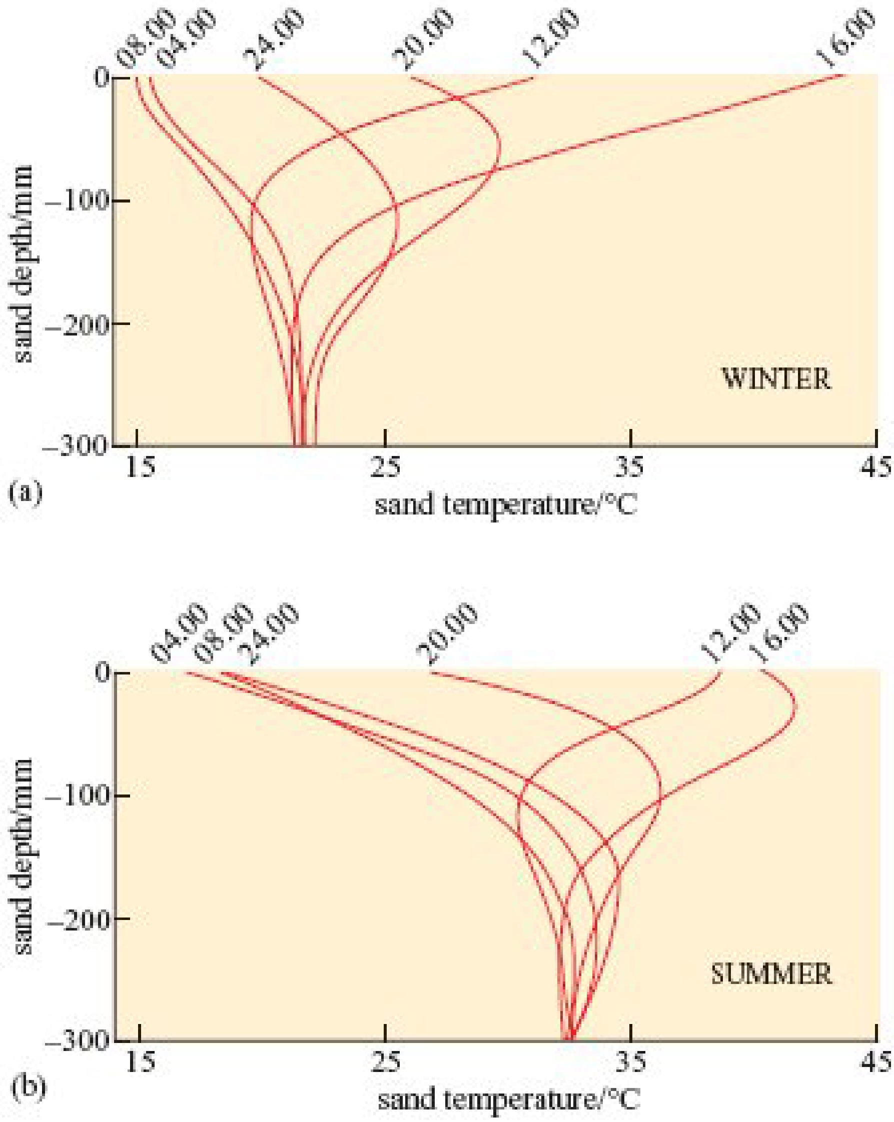

Figure 17 Temperatures below the sand surface, measured at 4-hourly intervals on a dune surface in the Namib desert in the (a) winter and (b) summer

Louw, G.N. (1993) Temperature and thermoregulation, *Physiological Animal Ecology*, Longman Group UK Ltd

Louw, G.N. (1993) Temperature and thermoregulation, *Physiological Animal Ecology*, Longman Group UK Ltd

Although the temperatures of sand at various depths in the Mojave desert would not be precisely the same as those in the Namib, the physical characteristics and thermal environment provided by dry sand are broadly the same in all deserts at similar T_a. A benign temperature is available below the surface at all times of the day in both seasons, in spite of extremes on the surface. These surface temperature extremes are not very different in summer and winter. The high afternoon surface temperature in winter is due to hot, dry winds (Berg winds) that reach the desert in the winter months.

Activity 3

Examine the data in Figure 17 and suggest the advantages for a sand-swimming lizard of the following strategies:

1. The lizard 'swims' down to 60 mm depth at 12.00 hours in summer, when surface temperatures can reach 40°C or more.
2. In winter, the sand-swimmer remains in a state of dormancy for a month at 300 mm depth in the sand, when surface temperature can occasionally drop below freezing at night.

Answer

1. At 12.00 hours, when T_a is 40°C at the surface, by burrowing to a depth of 60 mm the lizard reaches a microenvironment where T_a is significantly lower, about 32°C (Figure 17b). The lizard loses body heat by conduction and thereby avoids a dangerous increase in body temperature.
2. In winter when ambient temperatures can drop to below freezing, the temperature at 300 mm depth remains constant at around 21°C (Figure 17a). The lizard thereby avoids low T_a at the surface and is not at risk of freezing when T_a drops to < 0°C.

Burrows provide important microenvironments for many desert evaders, and their structure and use vary between species. The desert tortoise (*Xerobates agassizii*; Figure 18) lives in deserts in the USA and Mexico, and feeds on annual herbs, cacti and shrubs, obtaining most of its water from the plants.

Figure 18: The desert tortoise (*Xerobates agassizii*)

NHPA/Rod Planck

In the Mojave desert, the tortoises live in sandy areas as well as rocky hillsides, including scrub-type vegetation, joshua tree/yucca and creosote bush/ocatillo habitats. For the tortoises, burrows are important refuges for thermoregulation, summer aestivation and winter hibernation. Tortoise burrows in the Mojave desert are extensive and can be up to 12 m long; the same burrows are used for many generations, and are shared with other species such as burrowing owls and ground squirrels. Each desert tortoise may use up to 12 burrows in its home range and each burrow is used by different tortoises at different times. For short rest periods during the day tortoises dig shallow depressions, known as pallets, which barely cover the carapace.

Susan Bulova (2002) compared temperature and humidity in four unoccupied desert tortoise burrows, and the surface over 24 hours on a summer day in the Mojave desert (Figure 19a–c).