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Hot Deserts

Exequiel Ezcurra, *University of California, Riverside, California, USA*
Eric Mellink, *Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, Mexico*
Alejandra Martínez-Berdeja, *University of California, Riverside, California, USA*

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Introductory article

Article Contents

Hot deserts occur in two global belts north and south of the equator, at latitudes where calm air and a stable atmosphere dominate. Desert rainfall occurs in the form of highly unpredictable pulses followed by long periods of drought, and many plants and animals are finely adapted to these cycles of abundance and scarcity. Water-storing succulents and short-lived ephemeral plants are some of the most common life forms in these highly variable and strongly pulsating environments. In spite of their apparent barrenness, the hot deserts of the world harbour unique and rare biotas with impressive biological adaptations. As a result of evolution in isolation from each other, the world's deserts have high levels of endemism and harbour rare and unique life forms, a fact that makes them ecologically fragile and highly vulnerable to biological extinction.

Introduction

If one looks at a satellite image of the whole Earth it is easy to spot a series of conspicuously ochre-coloured, vegetation-barren areas that run parallel to the equator, in both the northern and southern hemispheres, along the two East–West fringes at 25–35° latitude in each hemisphere (**Figure 1**). They are the large subtropical deserts of the world, lying some 2000–4000 km away from the equatorial rainforests (Ezcurra *et al*., 2006; Ezcurra and Mellink, 2013). In the northern hemisphere, the succession of mid-latitude subtropical deserts is formed by (1) the Mojave, Sonoran and Chihuahuan Deserts in North America, (2) the Sahara's immense desert corridor in Northern Africa and (3) the deserts of Asia, including the Arabian and Thar drylands that cover all the way from the Middle East into Pakistan and India and the Gobi desert in China. In the southern hemisphere, the chain is formed by (1) the Atacama and Monte Deserts in South America, (2) the Namib and Kalahari in southern Africa and (3) the Australian drylands (Allan *et al*., 1993). Cold or mid-latitude deserts and steppes, occur at higher latitudes (35–55°), deep within the interiors of continents and separated from the windward coasts by mountain ranges, such as the Great Basin, in the United States, or the Patagonian Desert in Argentina. Although in hot deserts water deficit is present all year round, in cold deserts plant growth is limited by freezing temperatures in winter and by aridity only in summer.

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Deserts occur in these precise latitudes because of the general thermodynamics of our planet: Solar radiation hits the Earth with highest intensity near the equator. Because the Earth's axis is tilted 23.5° with respect to the plane of its orbit, during a part of the year, the zone of maximum solar interception shifts northwards, towards the Tropic of Cancer, and during the other part it moves southwards, towards the Tropic of Capricorn. Thus, the warm tropics form a belt around the equator from latitude 23°N to latitude 23°S, where the tropical heat generates rising, unstable air. As the rising air cools in its ascent, it condenses the moisture evaporated from the warm tropical seas and forests producing the heavy downpours that characterise the wet tropics. Having lost its moisture, the air moves in the upper atmosphere away from the tropical belt, and starts to descend around 25–30° latitude. This stable, dry air forms the mid-latitude arid fringes that run north and south of the tropical belt, forming corridors of stable atmosphere – known as the 'horse' latitudes – where calm air dominates. The closed circulation of air, ascending in the tropics into the upper atmosphere to descend in the subtropical latitudes and moving again towards the tropics, is known as the 'Hadley Cells' (in honour of the British climatologist George Hadley). Hadley Cells, the low-latitude overturning circulations that have air rising at the equator and sinking at 30° latitude, are responsible for the trade winds in the tropics and control low-latitude weather patterns. Because of the stable atmosphere in the polarward side of the cells, not only winds are slack but rainstorms seldom develop; and this is the reason why most of

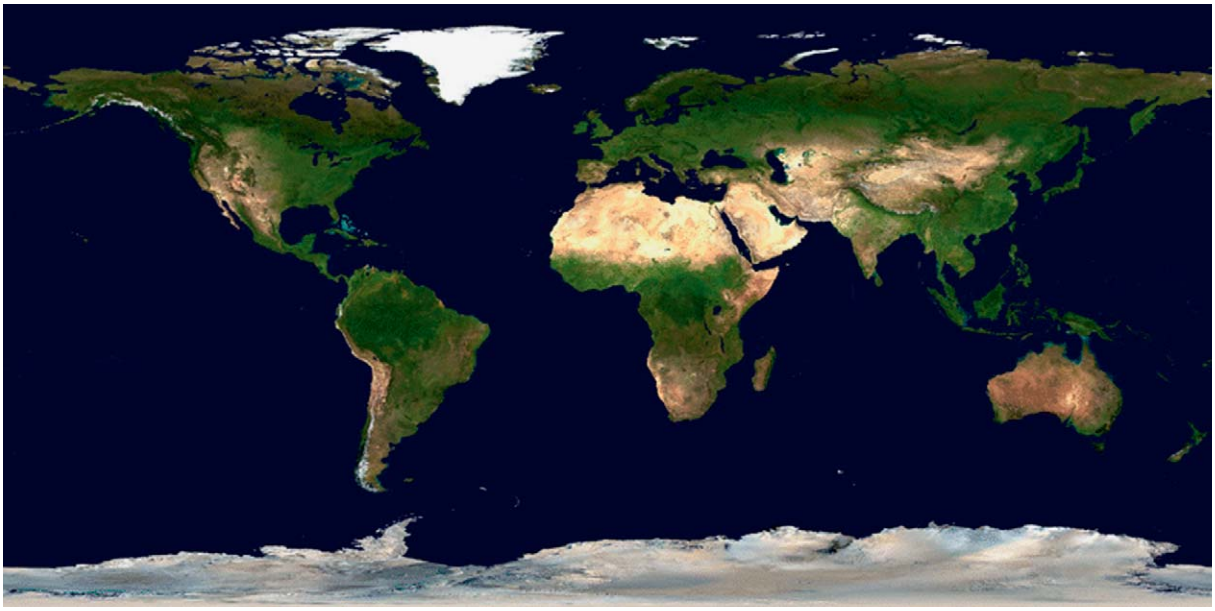

Figure 1 Satellite composite image of the Earth, showing the two hot desert belts north and south of the equator. Taken from NASA's 'Earth Observatory' website (http://earthobservatory.nasa.gov/). © NASA.

the world's large deserts occur at these latitudes both in the northern and southern hemispheres (Goudie and Wilkinson, 1977; McGinnies *et al*., 1977).

The previous explanation, however, tells only a part of the story. Gravitation from the sun and the moon pulls air and water on the Earth's surface and tends to make them lag behind, relative to the Earth's rotational movement. The gravitational drag is greatest in the equator, where the centrifugal speed of the Earth is fastest. Thus, as the Earth turns, ocean currents and winds flow in the equator from east to west, tugged by external gravitation, forming the equatorial currents and the easterly trade winds. As the westbound surface waters move away from the continents, they pull cool, nutrient-rich waters to the surface that generate a cool, stable coastal atmosphere, with little evaporation from the sea, low rainfall and morning fogs. The large-scale circulation of the ocean is the reason why coastal deserts are always found in the west side of continents, such as the Namib in Africa, Atacama in Chile or the deserts of Baja California.

Topographic heterogeneity also contributes to the formation of drylands, especially within the tropical belt. When the moisture-laden tropical trade winds reach continental mountain ranges they cool as they ascend, condensing as fog and drizzle that feed montane cloud forests. Once the winds pass the mountain divide, they start compressing and warming-up again in their descent, but, having left behind their original moisture, they become hot and dry. Thus, although the windward slopes of most tropical mountain ranges are covered by cloud forests, the Leeward part, also known as the 'rain shadow' of the mountains, is covered by arid scrubs. The rain shadow effect is largely responsible for many tropical drylands, such as the Caatinga scrubs in equatorial Brazil, or the Tehuacán Valley desert in southern Mexico, a hotspot for cactus biodiversity.

Desert Sky-Islands and Climates of the Past

During the last 2 million years (the Pleistocene period), the Earth underwent a series of alternative cycles of cooling and warming, induced by variations in the planet's orbit and in the inclination of its axis. During the colder periods – known as the 'Ice Ages' – most of the high-latitude regions of the world became covered by massive glaciers and temperate ecosystems such as cold grasslands and conifer forests moved southwards. During these glacial periods, the tropical belt narrowed and the mid-latitude hot deserts shrunk replaced by grasslands, semiarid scrubs and open woodlands. The desert biota found refuge in dry subtropical valleys where arid conditions persisted under the rain shadow of large mountain ranges. The last glaciation ended approximately 15 000 years ago, and we are still living in the warm interglacial period that followed – the Holocene.

When the ice sheets started to retreat (20 000 years ago), most of the temperate flora and fauna started to move back into higher latitudes. A subset of those species, however, managed to survive in the mid-latitude regions by climbing up the rugged and cool mountain ranges that emerge like islands from the desert plains. Establishing higher-up with each passing generation as the climate warmed, the ice-age organisms were able to persist in the cool mountain environments where they found a climate similar to the one they had enjoyed in the lower plains during the ice ages.

As they ascended into the isolated desert mountains, the communities of the desert 'sky-islands' became separated from the other mountains by a sea of harsh desert plains. Like antediluvian castaways, the ice-age species now survive high-up in the cool refuges of the desert mountains. The mediterranean scrubs and pine forests of the Atlas Mountains in the Moroccan Sahara, or the temperate forests that prosper in the mountains that dapple the Chihuahuan Desert in North America, are two of the many magnificent examples of these relictual ecosystems; a biological memory of bygone evolutionary history surviving high-up in the mountains like a ghost of climates past (Dimmit, 2000).

Cycles of Abundance and Scarcity

The intensity of ocean upwellings and rain shadows, the two major factors modulating the distribution of arid lands, is not constant but may vary from one year to the next. This was noted many years ago by the fishermen and the farmers of the coastal desert of Peru, who realized that during some years, the normally cold waters of the Pacific became warmer. In these years, they noted, the abundance of sardine decreased, but abundant rainfall soaked the land and made the desert flourish. Because this warm current was often observed around the month of December (a time of the year in which Christians commemorate the birth of Jesus Child – *El Niño* in Spanish), they called the phenomenon 'El Niño'.

During El Niño years, the trade winds and the equatorial currents slacken their westward flow, and the upwelling of nutrient-rich waters decreases. The sea becomes less productive, whereas the coastal deserts become often drenched in the abundant rainfall that originates from the now warm sea waters. These pulses of abundance and scarcity of resources are a major force in the ecological organisation of many deserts of the world. During pulses of bounty, the fragile seedlings of desert plants can germinate, establish and prepare for long droughts burying their roots deep into the desert soils. Ephemerals can replenish their seed banks, desert toads can reproduce in extraordinary numbers before entering again into their waterless torpor and granivorous rodents, such as North American kangaroo rats, Australian hopping mice and African jerboas, can stock up their underground caches. The desert becomes renewed, and ready to face again years, or even decades, of extreme hardship.

Winter and summer rainfall patterns

Two important weather systems bring precipitation to the world's deserts. The horizontal transport by wind of moist air from the sea onto the land (known as advective transport) during winter, when the land becomes colder than the sea, causes atmospheric condensation over the cold continents and generates winter rains. Because this particular pattern of summer droughts and winter rains dominates the coasts around the Mediterranean Sea, the areas of the world that show this type of seasonal variation are called 'mediterranean' regions. In summer, in contrast, a different weather system is the main driver of rainfall pulses in arid lands. As the continents become hot they generate low-pressure centres with rapidly ascending warm air (a phenomenon known as convective transport). As the air ascends, the atmospheric mass cools rapidly and condenses large amounts of air moisture, which pour down in the form of summer thunderstorms. In many parts of the world this rainfall pattern is known as the 'monsoon'.

Most of the large deserts of the world lie between these two weather patterns. The large mid-latitudinal deserts often share their boundary with winter-rain mediterranean ecosystems in their higher latitudes, and with monsoon regions near their tropical reaches. The Sahara Desert, for example, is dominated by winter rains in its northern Mediterranean limit, and by summer rains in its more tropical Sahelian border. The Sonoran Desert, in North America, receives mostly winter rains in its northwestern reaches, near the Mojave, and is fed by the Mexican summer monsoon in its tropical southern reaches (Robichaux, 1999; see **Figure 2**).

Plants in winter-rain deserts have a rather narrow window of opportunity for growth. During winter, moisture accumulates in the soil but the weather is often too cold for plant growth. During summer, temperature may be

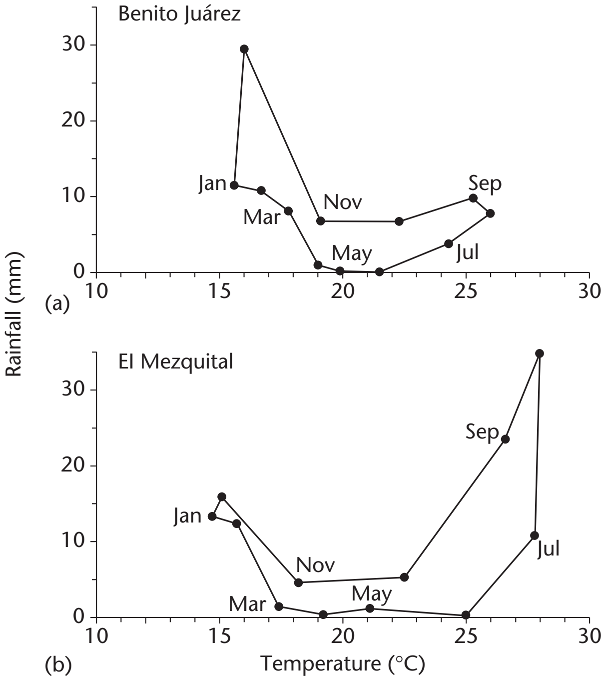

Figure 2 Only 40 km apart, two weather stations in the deserts of the narrow Baja California peninsula show the effect of oceanic currents on winter and summer rains: In Benito Juárez, near the Pacific coast and under the influence of the California Current, rains come during the coldest months of the year (a). In El Mezquital, near the hot Gulf of California and facing the continental mainland, rains arrive in summer in the form of tropical thunderstorms (b).

adequate but the soil is parched and waterless. Only during spring, when temperatures start to rise and moisture is still present in the ground, plants can flourish. Thus, the winter-rain deserts of the world are amazingly rich in short-lived spring ephemerals. These plants survive the scorching summer in the form of seeds, bulbs or tubers, and quickly sprout during the narrow window of opportunity that the desert spring provides. In monsoon deserts, in contrast, rainfall pulses coincide with adequate temperatures for plant growth. In these deserts, perennial plants often show extensive networks of shallow roots, as many plants compete to extract water from the soil immediately after the rain has fallen. Giant fleshy trunks or cactoid succulent stems, adapted to accumulate water, are common in summer-rain deserts.

Life Forms and Adaptations

In its origins life evolved in water, and water is the most crucial element for the survival of all organisms. Thus, it is no surprise that some of the most remarkable adaptations for survival are found in desert species, that is, in the environments where water is most scarce (Louw and Seely, 1982). The short pulses of abundance that contrast sharply with the background condition of aridity and scarcity are the major force that has driven evolution, natural selection and adaptation in desert biota. Plants and animals are adapted to these seasonal strokes. Natural selection and evolution have moulded in very precise ways the life forms of desert organisms to their harsh and unpredictable environment. Furthermore, because most deserts of the world have evolved recently and in relative isolation from each other, many of their constituent species have evolved from different ancestors (Morton, 1979). Thus, deserts are prime ecosystems to study and understand the phenomenon of convergent evolution – the development of similar growth forms and adaptations derived from different ancestors (**Table 1**).

Adaptations of plants to aridity

Most desert species have found remarkable ways to survive by evading drought. Desert succulents, such as cacti or rock plants for example, evade dry spells by accumulating moisture in their fleshy tissues. They have an extensive system of shallow roots that allows them to capture soil water only a few hours after it has rained. Their photosynthesis is modified to exchange gases and fix carbon dioxide (CO_2) during the night, when evaporative demand is low, and to accumulate the fixed carbon in the form of malic acid, which is later used by the plant as the building blocks of more complex organic molecules (this photosynthetic pathway is called 'Crassulacean Acid Metabolism' or CAM). Additionally, many cacti and other stem-succulent plants of hot deserts present columnar growth, with leafless, vertically erect, green trunks that maximise light interception during the early and late hours of the day, but avoid the midday sun, when excessive heat may damage, or even kill, the plant tissues. Thus, erect columnar plants may avoid drought by (a) accumulating water, (b) exchanging gases at night and (c) morphologically avoiding mid-day exposure to solar radiation.

Woody desert trees, such as acacias, cannot store much water in their trunks, but many of them evade drought by shedding their leaves as the dry season sets-in, entering into a sort of drought-induced latency. Many of these desert species also have deep pivotal roots that allow them to tap into the desert's aquifer, the underground water layer accumulated deep beneath the soil. Other trees have convergently evolved a mixture of these strategies: they can store water in gigantic trunks and have a smooth bark that can do some cactus-like photosynthesis during dry periods. When it rains, however, they produce abundant green leaves and shift their metabolism towards that of normal-leaved plants. This group is formed by trees with famously 'bizarre' trunks, such as the African baobab (*Adansonia*), the Baja-Californian Boojum-tree (*Fouquieria columnaris*) and elephant-trees (*Bursera* and *Pachycormus*) and the South African bottle-trees (*Pachypodium*).

A third group of plants, the 'true xerophytes' or true desert plants, have simply adapted their morphology and their metabolism to survive extremely long droughts. These species have remarkably low osmotic potentials in their tissue, which means that they can still extract moisture from the soil whereas most other plants cannot do so. True xerophytes, such as the creosote bush (*Larrea*), are mostly shrubs with small, leathery leaves that are protected from excessive evaporation by a dense cover of hairs or a thick varnish of epidermal resin. Their adaptive advantage lies in their capacity to extract a fraction of soil water that is not available to other life forms. However, because their leaves are so small and protected from transpiration, their gas-exchange metabolism is very inefficient during rain pulses, when moisture is abundant. In consequence, these species are extremely slow growers but very hardy plants.

Finally, one of the most effective drought-survival adaptations for many species is the evolution of an ephemeral life cycle. Selection for a short life and for the capacity to leave behind resistant forms of propagation is perhaps one of the most important evolutionary drivers in most deserts, found not only in plants but also in many invertebrates. Desert ephemerals are amazingly rapid growers capable of reproducing at a remarkably high rate during good seasons, leaving behind myriad resistance forms that persist during adverse periods. Their population numbers simply track environmental bonanzas; their way to evade critical periods is to die-off, leaving behind immense numbers of propagules (seeds or bulbs in the case of plants, eggs in the case of insects) that will restart the life cycle when conditions ameliorate. These opportunistic species play an immensely important role in the ecological web of deserts: A myriad organisms, like ants, rodents and birds, survive the dry spells by harvesting and consuming the seeds left behind by the short-lived ephemeral plants. Granivory (the consumption of seeds) and not herbivory

Table 1 Convergent evolution of animal guilds in four hot deserts of the world. In spite of their different phylogenetic origin and their different biogeographic histories, many of these animals look strikingly similar in appearance

	Deserts			
Guild	North American	Australian	North African	South African
Bipedal rodent granivores[a]	*Dipodomys*	*Notomys*	*Jaculus*	
Quadrupedal rodent granivores[a]	*Chaetodipus* *Perognathus*		*Taterillus* *Pachyuromys* *Gerbillus* *Sekeetamys*	*Gerbillus* *Tatera* *Gerbillurus*
Small rodent insectivores[a]	*Onychomys* *Notiosorex*	*Antechinus* *Sminthopsis* *Antechichomys*	*Crocidura*	*Crocidura* *Elephantulus* *Macroscelides*
Mid-sized herbivores[a]	*Lepus* *Sylvilagus*	*Onychogalea*	*Lepus*	*Pedetes*
Mammalian carnivores[b]	*Vulpes*		*Fennecus*	
Ant-eating reptile[b]	*Phrynosoma*	*Moloch*		
Horned snakes[b]	*Crotalus*		*Cerastes*	*Bitis*
Open-space, long-legged lizard[c]	*Callisaurus*	*Amphibolurus*		
Medium-sized, lizard-eating lizard[c]	*Crotaphytus*	*Varanus*		

[a] Mares (1980).
[b] Schmidt-Nielsen (1964).
[c] Pianka (1986).

(the consumption of leaves) is at the base of the food chain in most deserts, as those few plants that maintain leaves during dry spells usually endow them with toxic compounds or protect them with spines. The onset of rainy periods brings to the desert a reproduction frenzy of desert annuals, and a subsequent seed-pulse that drives the entire food web for years.

Coping with unpredictability

In most deserts rainfall is not only scarce but also highly unpredictable (Noy-Meir, 1973). Desert annuals have developed precise evolutionary responses to cope with environmental unpredictability by avoiding taking excessive risk when a single rain falls. These ephemeral plants spend most of their life cycle as seeds, and germinate and grow only when there is available moisture. But a false signal, like a single rain not followed by additional moisture, can drive all the seeds that germinate following that false queue to die before reaching reproductive age. To avoid this risk, most desert annuals have evolved fractioned germination, where not all the seeds of a cohort will germinate following a water queue. Some will germinate easily with the first rain, and, if more rains continue, they will have a competitive edge of having taken early advantage of available water. Others will not germinate with a single rain, but may require successive rains to accumulate enough moisture in the environment. These more prudent germinators will not have the adaptive advantage of early sprouters, but will face none of the risks of a false rain queue. For a single plant, producing highly variable seeds, ranging from quick sprouters to extremely cautious germinators will increase its chances of survival in extremely unpredictable deserts (Gutterman, 1993; Mulroy and Rundel, 1977).

Timing of seed dispersal also allows desert annuals to cope with environmental variability. Many desert plants retain the seeds within the maternal tissue in capsules or dry fruits, and release them gradually into the risky desert environment only when enough moisture softens the seed-retaining structure. Serotiny – the ability to retain seeds in the mother plant – allows plants to reduce risk by retaining seed safely within protected maternal structures and releasing them gradually into the environment as rains arrive. **See also**: Seed Banks and Gene Banks

Finally, although plants in more predictable environments have well defined life-history phases (seedling, sapling, vegetative and reproductive phases), many desert plants start producing flowers shortly after germination and keep on flowering as they grow, until the resumption of dry conditions ends their ephemeral life. If the rainy season is short, they will produce at least a few fruits, and if the rainy season continues they will opportunistically keep on producing seeds to replenish their seed banks and reinitiate their ephemeral life cycle when future rains arrive.

Adaptations of animals to aridity

Behavioural adaptations

To the physiological, anatomical and morphological adaptations of plants, animals can add adaptive behaviour (Schmidt-Nielsen, 1964). Many birds and most large mammals, like pronghorn antelopes or wild sheep, are capable of evading critical spells by migrating along the desert plains or up into the cooler mountains. Smaller animals cannot migrate such long distances, but regulate their environment by seeking-out cool or shady places. In addition to flying to other habitats during the dry season, birds can reduce heat loads by soaring. Many rodents, invertebrates and snakes avoid heat by spending the day in caves and burrows, and procuring food during the night. Even diurnal animals may reduce their activities by resting in the shade during the hotter hours of the day. Fossoriality, a lifestyle based in burrows, is the norm for small animals in all deserts, as it allows them to stay away from the gruelling heat during the hotter part of the day and it also provides them a warm refuge during the cold desert nights. Additionally, high air moisture inside burrows (approximately 30–50%) allows desert animals to preserve water. When the normal mechanisms to keep body temperature within acceptable limits fail, many small rodents and some desert tortoises (*Testudo*) resort to salivation to wet the chin and throat and allow evaporative cooling. Such mechanisms have a high cost in water and are used only as emergency measures to prevent death. **See also**: Fundamentals of Water Relations and Thermoregulation in Animals

At dawn, the dry desert ground may approach freezing temperatures and at midday it may heat up into an 80°C inferno. A few inches above the ground, variations in air temperature are much less pronounced, and, just a few inches below the surface, underground temperatures are almost constant between day and night. For this reason, thermoregulation is a particularly challenging problem for small surface dwellers, and especially for reptiles, which cannot regulate their body temperature metabolically. Many desert reptiles have developed peculiar ways of travelling over hot sandy surfaces. Side-winding, a form of lateral movement in which only a small part of the body is in contact with the surface at any given time, is employed by many sand snakes. Many lizards are capable of running rapidly over the hot desert surface, maintaining their bodies separated from the ground and often assuming an erect, bipedal position. Other lizards regulate their contact with the hot desert pavement by doing ‘push-ups’ with their forelegs.

Large mammals that cannot avoid being in the sun during a large part of the day often orient their bodies so as to reduce the incidence of the sun’s rays. By standing upright, guarding ground squirrels reduce solar incidence upon their bodies. The African squirrel *Xerus inauris* even orients towards the sun and shades itself with its tail when foraging. The jackrabbit *Lepus californicus* warms its body in the early morning by exposing its large, highly vascularised ears to the sun’s rays, and cools at midday by keeping in the shade and putting the ears parallel to the incoming solar radiation, thus minimising exposure while keeping the same radiative surface.

Morphological and anatomical adaptations

In mammals, desert fur coats are short, hard and compact, but at the same time well ventilated, especially in large mammals, to allow for sweat to evaporate directly from the skin. Birds, in addition, can fluff or compact their feathers at will, thus regulating heat exchange. In ostrich, a strict desert dweller, the uncovered head, throat, legs and abdomen allow for radiation and convection cooling, whereas the feathers on the back protect the larger part of the body from direct solar radiation. Bipedalism, a common trait in small deserts mammals such as kangaroo rats, allows for fast travel in open spaces and also keeps the body separated from the extreme temperatures of the ground layer. Indeed, bipedal desert rodents use open microhabitats much more frequently than their quadrupedal relatives, who restrict their activities to sheltered habitats.

Sand-dwellers have evolved several traits that allow them to survive in dunes, including fleshy foot-pads in camels, scaly fingers in certain lizards and digital membranes in some geckoes. Additionally, camels have long dense lashes that protect their eyes and they can close their nostrils to protect them from wind-blown dust. Many snakes have rostral adaptations that allow them to burrow rapidly in loose sand, and upwardly turned nostrils; others are flat and can bury laterally. Many other reptiles also show adaptations to protect their eyes, nose and ears from sand and dust, and many insects have especially adapted legs that allow them to bury themselves rapidly and to walk efficiently on the hot sand (Pianka, 1986).

Because of the high evaporation, saltflats are a common environment in hot deserts. For animals, survival consuming salty plants is particularly challenging, as a large physiological effort is needed to get rid of the excess salt. At least four rodent species from salt basin desert habitats throughout the world (one each from South America, North America, Asia and Africa) share specialised adaptations to live on a diet of salt-laden plants. These adaptations include chisel-shaped lower incisors to strip away salty epidermises, specialised kidneys that maximise urine concentration capacity and, in one case, bristles at the sides of the mouth to scrape salt off leaves (Mares, 1980).

Physiological adaptations

The most basic physiological problem of desert animals is that of maintaining their water balance by maximising water intake and/or minimising water loss. In deserts, free-standing water is scantily found in isolated oases and rain-fed reservoirs. Camels and wild asses, for example, can drink large quantities of water in a very short time causing a dramatic dilution of the bloodstream, sufficient to cause death in other animals. In coastal deserts, animals obtain water by licking fog-saturated rocks. Desert amphibians can absorb water through the skin from humid underground dens by accumulating urea in their blood and raising its osmotic pressure. **See also**: Fundamentals of Water Relations and Thermoregulation in Animals; Vertebrate Metabolism in Extreme Conditions

Most herbivores, like elands and oryx, obtain water from the foliage of the shrubs that compose their diet, often feeding at night when the plants are turgescent. Some succulent plants have high salt contents, toxic compounds or spines that make it difficult for their consumption. Herbivores, however, have found their way around these obstacles: some reptiles and birds have developed efficient salt-excreting glands, and many mammals have kidneys that can cope with salty water. The white-throated pack-rats (*Neotoma albigula*), which feed almost exclusively on juicy cacti, have metabolic adaptations to prevent intoxication from the oxalates contained in these plants.

Animals lose water through urine, faeces, respiration and transpiration. Desert rodents have kidneys that are capable of producing highly concentrated urine, with an electrolyte concentration many times higher than that of blood plasma. Reptiles, birds and insects excrete uric acid, which requires less water, and sometimes complement the excretion process with specialised excretion from salt glands. Amphibians produce little urine, and can store large amounts of urea within their bodies, drastically reducing water loss. Under drought, some rodents can produce dry faeces, efficiently reabsorbing liquids in the rectum.

Cellular metabolism produces CO_2 and water as byproducts of respiration. In most animals, this metabolic water is lost through breathing, but many desert animals, including invertebrates, reptiles and mammals, possess physiological and anatomical adaptations to reduce respiratory water loss, including modifications in the morphology of the nasal passages and the capacity to reabsorb water along the respiratory tract. One of the most extreme examples of this is given by the kangaroo rats (*Dipodomys*), which can survive on a diet of perfectly dry seeds.

In addition to the mechanisms that reduce water loss, many desert animals are extremely tolerant to dehydration, a condition that causes a fatal increase in blood viscosity in nondesert dwellers. Camels, for example, are able to lose water selectively from tissues other than blood. Desert amphibians are tolerant to increased fluid viscosity, and some reptiles can excrete excess electrolytes through urine and salt glands, avoiding the thickening of the blood as they dehydrate. A problem related to dehydration is that of temperature regulation. In smaller animals, the high surface-to-body ratio makes sweating a dangerous enterprise and panting is the most common method of cooling. Even larger animals that usually sweat, like the oryx, begin to pant when their body temperature exceeds 41°C.

Nocturnal hypothermia, exhibited by some large mammals like the eland allows them to reduce their metabolic rate and to exhale air with less humidity during the night. Diurnal hyperthermia allows animals to reach body temperatures that would be normally lethal for nondesert vertebrates and to save on water needed to prevent overheating. Camels and elands, for example, can reach 44°C with no harmful consequences, and save as much as 5–10 L of water during extremely hot days. Hyperthermal species have a special disposition of veins and arteries that allows their brains to remain at a temperature lower than that of the overheated body.

Like ephemeral plants, many smaller desert animals can also evade drought by entering into a dormant phase: Desert butterflies and grasshoppers thrive in huge numbers when conditions are good and survive dry spells in the form of eggs or pupae. Spade-foot toads (*Scaphiopus*) spend most of their lifetime buried in dry mud and become active only after rains refill their tanks. Many other organisms go into some form of torpor during dry periods. **See also**: Hibernation: Endotherms

Species Interactions

The harsh conditions of desert ecosystems have promoted the evolution of a complex set of relations among desert organisms, a surprising number of which are positive interactions. Desert shrubs in general, and woody legumes in particular, create microhabitats that are critical for the survival of other species. Small animals seek the shade of desert trees and shrubs, birds find refuge and nesting sites in their canopies and many small plants recruit their juveniles under the nitrogen-rich canopy of desert legumes such as acacias, carobs and mesquites. Because of their CAM metabolism, desert succulents such as agaves, aloes and cacti are poor thermoregulators as young seedlings, and cannot survive the harsh ground-level midday temperatures. For this reason, they can germinate and establish only under the protective shade of shrubby ‘nurse plants’ that act as true cornerstone species in desert conservation. If the desert trees and shrubs are cut, all the accompanying biota soon disappears.

Additionally, many desert plants have very specific requirements in terms of their pollinators and seed dispersers. Although some desert ephemerals are truly unspecific in their requirements and produce thousands of seed, the slow-growing desert perennials are frequently highly specialised in their reproductive habits, and depend strictly on coevolved animals to help them out in their sexual and reproductive processes. African succulent euphorbias produce foul-smelling flowers that attract carrion insects as pollinators. New World giant cacti and agaves produce sugar-rich nocturnal flowers that engage the pollinating services of nectar-eating bats. Red tubular flowers attract hummingbirds and giant sphinx-moths. The sweet pulp of prickly pears lures birds to disperse their seeds miles away.

Deserts and Agriculture

Because desert ephemerals grow so fast and produce so much seed in just a few weeks, it comes as no surprise that the earliest archaeological records of agriculture come from dryland regions and that the first domesticated crops evolved from desert annuals. Indeed, the first records of cultivated wheat and barley (two dryland ephemerals) come from the Fertile Crescent of the Middle East some 7000–9000 years ago. In the American Continent, the first agricultural records come from the Tehuacán Valley in southern Mexico, a hot tropical dryland where corn and squash (two annual, drought-tolerant fast growers) were first domesticated. To a large extent deserts have been the cradle of agriculture, and humans have been using desert environments for thousands of years (Cloudsley-Thompson, 1979, 1996).

Concluding Remarks

For the untrained eye, deserts look scrubby and poor in biological richness, especially during dry periods. However, because of their evolution in relative geographic isolation, most deserts of the world are rich in rare and endemic species, and are hence highly vulnerable to biological extinction and environmental degradation. In spite of their remarkable convergence in adaptation, all deserts are different in their origin and their evolutionary history (Pipes, 1998; Ricciuti, 1996).

The incredible variation of the world's deserts in rainfall patterns, continentality, temperature regime and evolutionary history have all contributed not only to their biological uniqueness, but also to their wondrous wealth of life forms and adaptations. This adaptive diversity – what Darwin, strongly influenced by deserts himself, called 'forms most beautiful and most wonderful' – is what makes deserts so unique. In the hot deserts, we may find giant cacti and trees with mammoth fleshy stems coexisting with some of the toughest hardwoods; ground-creeping succulents side by side with fog-harvesting rosettes, incredibly fast-growing annuals together with some of the hardiest drought-resistant perennials ever known; aromatic shrubs of enticing odours with some of the nastiest, spiniest plants ever. Very few places on Earth contain a richer collection of natural adaptations and such a unique array of evolutionary histories (Davis, 1998).

The fragmented evolutionary history of the deserts of the world has been the driving force of their biological rarity, of adaptation to local conditions, of specialisation to isolated environments. After millions of years in isolation, the forces of evolution and fragmentation have yielded unique life forms in each desert, strangely shaped desert plants and extraordinary animals. The world's deserts have been indeed almost biological and cultural islands, lands of fantasy and adventure, habitats of surprising, often bizarre growth forms and territories of immense natural beauty.

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