# ASPECTS OF THE BIOLOGY OF DESERT ORGANISMS

The extreme nature of desert environments presents a myriad of problems to the plants and animals that inhabit them. But just as there are a variety of problems, there are also a great number of solutions to these difficulties. Desert animals and plants fascinate and amaze me with their adaptations, which in some cases, are quite complex. In others they are simple, even though they solve complex problems.

Just a few of the adaptational problems faced by desert species are listed below. In fact many species have developed adaptations to several of these problems, and some individual adaptations solve more than one problem. Remember that one of the most common adaptations to desert conditions is simply to avoid its rigors altogether.

Some of the problems are these: 1. Water is in low supply most of the time. When present, it often occurs in floodlike quantities. 2. Water occurs at unpredictable intervals and in unpredictable quantities. 3. Summer daytime temperatures may be extremely high. 4. The difference between daytime and nighttime temperatures may be extreme. 5. Loose substrates, which are easily blown about and difficult to traverse, may dominate the landscape. 6. Because vegetation is sparse and open, concealment from enemies is difficult, and there is little protection against the harsh environment.

## Plants

We are used to seeing trees, shrubs, flowers, and cacti in deserts. It may be surprising, however, to realize that algae and fungi occupy deserts as well, since these plants are usually thought to inhabit moist areas. Actually, certain algae and fungi, as well as lichens—the symbiotic outcome of the association of the other two—may be significant elements in the desert landscape.

### Nonflowering Plants

Algae—both green and blue-green forms—are common in the surface soils of deserts. More than one hundred species are known to inhabit the deserts of North America. Their prevalence is often inversely related to the proportion of land area covered by taller plants: Where shrubs are common, algae are not as abundant. The number of soil algae also decreases with depth. Virtually no algae are found twenty inches below the surface of the ground.

The algae in deserts survive the high temperatures and low water levels as a result of their physiological durability. Algae preserved in dry soil for over fifty years may remain viable, "greening up" when they come in contact with water. These microorganisms have certain advantages because of their small size. Because they can live in the spaces between soil particles, they can derive moisture from the dew condensed on the soil surface out of the cool night air, or from condensation within the soil pores themselves. They may even obtain the water that condenses under rocks. An interesting example of this desert adaptation can be seen by picking up a somewhat translucent rock, such as quartz, that is exposed at the surface of the desert soil. Often the sides and bottoms of such rocks are



covered with algae. These plants receive sufficient light *through* the rock to carry on photosynthesis, and they use as a source of water the moisture on the underside of the rock.

In addition to occurring in the soil and under rocks, algae can also be found in rock crevices and, astonishingly, within the very fabric of the rock itself. In both of these cases, water is made available to the plants, and the rocks provide protection, to some extent, from extreme heat.

Fungi occur in desert soils, and in part are responsible for the development of crusts on the soil surface. If you wish to examine a crust, you can, with care, remove a hand-size chunk that is up to an inch thick. Microorganisms, including algae, fungi, and lichens, bind the soil particles together with their "bodies"; this helps to hold down soil erosion.

More commonly recognized, above-ground, mushroom forms of fungi also occur in deserts. Such species include the common Desert Inky Cap, which occurs practically worldwide in desert areas that are as low as sixty-five feet below sea level. A species of more northern distribution is the Desert Stalked Puffball, which ranges as far north as Alaska. Another species, the Buried-stalk Puffball, is most common in sandy areas, including sand dunes.

Desert Inky Cap
*Podaxis pistillaris*
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Desert Stalked Puffball
*Battarrea phalloides*
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Buried-stalk Puffball
*Tulostoma simulans*
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Some fungi form a symbiotic relationship with higher plants. The structure resulting from this association, called a mycorrhiza, resembles root hairs and occurs in the same place on plants as roots do. The association helps the plant take up water and phosphorus. Many desert shrubs, trees, and flowers have such an arrangement; indeed, virtually ninety percent of all plant species worldwide are involved in these mycorrhizal associations. Scientists are studying this relationship with great intensity. One reason for such studies involves the difficult task of reestablishing plants in arid lands that have been used for mining. In cases where the plants being used for restoration are mycorrhizal species, it is important that the fungus be locally available to form the mycorrhizae. Such plants will fare much better in the harsh environment when the proper fungus exists and the symbiosis develops.

Lichens are quite abundant in deserts, both on the soil surface and when attached to plants in areas where fog occurs. They are also found on rock surfaces on the upper portions of bajadas. The lichens and algae that form soil crusts can capture nitrogen from the air. They put the nitrogen compounds required for plant growth into the biological cycle and, as a result, improve soil fertility. During times of the year when moisture is available, it "activates" the crusts, stimulating high rates of biochemical activity.

Other nonflowering plants may be common on certain specialized desert sites. Ferns occur in rock crevices or beneath the edges of boulders, places that funnel water to the plant. Such strategic locations, which also reduce insolation, help the fern to survive the desert's rigors. Desert ferns have adapted to tolerate repeated and prolonged dehydration; in addition, they are covered with "hairs" that reflect light and may thus insulate the fronds. Both of these strategies aid survival. The

Resurrection Plant
*Selaginella lepidophylla*

capacity to rehydrate following prolonged desiccation is a rather spectacular adaptation in a fern ally, the Resurrection Plant of the Chihuahuan desert.

Mosses occur sporadically in deserts. You may walk for miles and never see one, and then suddenly be surrounded by them. They are often concentrated in small mats beneath shrubs or under cactus clumps. While they frequently look dried and dead, simply spitting on them will revitalize many species before your eyes, revealing—as if by magic—the green, photosynthetically active tissue.

## Annuals

Annuals, or ephemerals as they are often called, cannot withstand drought. When dry conditions occur, the plant shrivels and dies. It is the function of the seed to withstand dry periods and to be the source of the next generation. Thus, these plants, which are so very characteristic of the desert, evade the worst of desert conditions.

North American desert annuals fall into two broad groups that coincide with the seasons of maximum rainfall. Thus winter annuals are those that respond to precipitation occurring in late fall, winter, and early spring, while summer annuals respond to the precipitation in summer and early fall. The hot deserts vary in their seasonal rainfall characteristics, and, as a result, so do the concentrations of the various annuals. The Mojave Desert is primarily a winter-annuals area; the Chihuahuan Desert, a summer-annuals area (plate 31); and the Sonoran Desert, with its biseasonal rainfall peaks, contains both winter and summer annuals (plates 32 and 33). The Great Basin Desert exhibits a paucity of native annuals, but, as one would expect, those that do occur are of the winter type.

The adaptation of annuals involves more than their ability to germinate in response to a particular pattern of seasonal rainfall. In contrast with winter annuals, summer annuals are taller, tend to be more weedy (to occur in disturbed sites), include many grasses, and have leaves that do not exhibit typical desert adaptations.

Of particular significance is a difference in the chemical pathways by which photosynthesis occurs in these two groups. Two types of photosynthesis are recognized. Plants of one photosynthetic group are termed $C_4$ plants. This name derives from the number of carbon molecules (four) in the specific chemical produced by photosynthesis. The other common group includes plants whose photosynthetic product (at an early stage) is a three-carbon chemical ($C_3$ plants).

Most summer annuals are $C_4$ plants, while most winter annuals are $C_3$ plants. $C_4$ plants carry on photosynthesis more effectively at high temperatures and high intensities of light, use water more efficiently, and produce more material than $C_3$ plants do under the same extreme conditions. $C_3$ plants, on the other hand, germinate during cool periods, often forming rosettes of leaves that hug the ground. Such rosettes may heat up quite a bit, even during cold periods, because they are at the ground surface. When the air warms later in the year, the ground surface is too hot for leaves, so these species frequently change their form and "grow up" out of the soil's surface, leaving behind its microclimate.

$C_3$ and $C_4$ plants also differ morphologically (in terms of their form and structure). To dissipate heat, the leaves of $C_4$ species are often subdivided into leaflets, or have serrated margins. $C_3$ species more often have simple (single-bladed), entire (nonserrated and nondivided) leaves. There are also internal anatomical differences that are not obvious to the unaided eye, and which we will ignore here.

The amount of rainfall greatly affects the relative abundance of annuals in different years. In general, more rainfall produces more annuals. But the situation is more complex. Winter and summer annuals both have a mechanism, involving a response to temperature and day length, that limits germination to the right time of year. This can protect a plant from responding to an unusual, potentially lethal, weather situation—one that gives favorable cues that might induce premature germination. If a winter annual were fooled into germinating by a summer rain, it might succumb to the high temperatures of the summer days—a situation to which it is not adapted. The detailed interactions of all of these environmental factors, and their effects on the germination of desert annuals, constitute an area of scientific inquiry at this time. Until explanations are forthcoming, suffice it to say that when conditions are just right, the desert bursts into a spectacular bloom.

Creosote Bush
*Larrea tridentata*
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The spatial pattern formed by adjacent annuals and perennials is also different for $C_3$ and $C_4$ plants. Winter annuals occur widely across sites, while summer annuals are more often found in the spaces between shrubs. Loosely canopied perennials such as palo verde and Creosote Bush harbor more annuals than do shrubs forming tight canopies such as bur sages (*Ambrosia*).

Certain early studies suggested that some plants might produce chemicals that inhibit annuals from growing under their canopies. This chemical inhibition of one plant by another is termed allelopathy. Allelopathic chemicals are often hypothesized or inferred to have a significant influence in desert systems. However, since some shrubs often have annuals in their shade, and certain annual species are virtually always found under shrub cover, the real importance of allelopathic chemicals in nature is still a matter of scientific debate.

One final adaptation should be mentioned. It is clear that if all the seeds of a particular species germinated under favorable conditions and then a disaster occurred, the species might not have time to reproduce. As a result, the species would be lost until other seed arrived from surrounding areas. To prevent this situation, not all seeds of the same species germinate synchronously. Thus, while many seeds germinate under favorable conditions, a number of seeds are reserved in the soil for another "good" time. This certainly underlines the fact that while annuals avoid desert conditions, this "avoidance" is based on numerous highly adapted mechanisms.

Perennials

Since perennials, by definition, must live for more than one growing season, they cannot escape the dry conditions of the desert in the same way that annuals do. It is true that the seeds of perennials give them a hedge against repeated bad years, which might ultimately kill mature plants, and that, in this way, they perform much like the seeds of annuals. However, it is the shrubs or trees themselves that must endure the desert conditions—and to which we turn our attention.

Perennials have a variety of strategies to survive drought situations. One group of species is referred to as the drought-avoiding water-savers. These species usually have one or more structural adaptations that cause them either to lose water more slowly or to store water when it is available. Among the more common adaptations are thick leaf or stem coverings (cuticles), which seal water in the plant; reduced exposure of the plant's surface area to the air, which minimizes drying; and succulent tissues with the capacity to store water. Cacti provide good examples of all of these modifications.

When you look at a cactus plant, you are actually viewing a stem—the fleshy portion of the plant—that is covered with the remnants of leaves—the spines. By being leafless, the cactus has reduced its total surface area and thus does not lose water at as high a rate as a leafy plant does. The tissues that in its extinct forbears formed leaves have been modified into spines. These may keep some animal predators away, and they also insulate the stem surface from solar radiation.

In some temperate species of cacti, leaves develop for a short period. Such leaves are small and short-lived, and thus are seldom seen by the the casual visitor.

Saguaro
*Cereus gigantea*
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Virtually the whole center of a cactus (the pith), as well as the outer perimeter (the cortex), are composed of water and food-storing tissues. A woody support material exists between these two layers and can be seen in the form of the intricately sculpted pieces of cholla skeletons lying on the ground in the hot deserts, or of the long, spearlike ribs of the Saguaro in the Sonoran Desert.

The water-impervious cuticular waxes are best developed on the sunny side of a cactus. In highly exposed species, such as the tall, columnar Saguaros, the differences in the wax thickness on various portions of the plant can be very significant. If you were to purchase a large Saguaro to be transplanted to your yard, you would want to make sure that it was replanted with its sunny side—the side with the thick cuticle—facing the sun. If you were to reverse the sides, the plant could be burned. Such damaged areas might make the Saguaro vulnerable to attack by fungi, which would cause its tissue to rot. Subsequently, the plant would die or, at the very least, its body would be deformed.

Another adaptation of cacti is to keep their stomates closed during the hot day. Stomates are the pores in the surfaces of leaves or stems, which allow plants to take in or give off gases, and through which water, usually taken up from the soil by roots, is lost. Most plants open their stomates during the day. In deserts, cacti open their stomates during the cool of the night instead and thus decrease the amount of water lost.

This adaptation creates another problem. To manufacture food, plants change carbon dioxide and water into sugar. Part of the complex series of reactions necessary to do this must be performed in the presence of light. Since the cactus takes up its carbon dioxide at night, in the dark, it cannot complete photosynthesis. Instead, in contrast with the chemistry of most other plants, the cactus takes up the carbon dioxide and then produces and stores an acid compound known as malic acid. This substance is later used to complete the food-manufacturing process during the day, when light is available but the stomates are closed. This specialized chemical system is called crassulacean acid metabolism, or CAM for short. The name is derived from a plant family—the Crassulaceae, or stonecrops, which contains a host of succulent species familiar to most peoples as hen-and-chickens, bryophyllums, or sedums—all of which possess CAM. In fact eighteen families of plants and more than 110 genera have species that use CAM. Most of these are succulents. In the American deserts, in addition to the cacti, both yuccas and agaves have CAM.

The shallow, broadly spreading root systems found in most species of cacti represent yet another adaptation. This feature allows cacti to take up water, even from light rain.

Some cacti use several adaptations. They avoid drought and save water by taking up water rapidly (shallow roots), storing large quantities (succulent stems), and sealing it off from the air (impervious cuticles, low surface area of stems, leaflessness, and practice of opening stomates at night).

A different desert-plant strategy, as unlikely as it may sound, is to be a water spender. Phreatophytes, the species that have this adaptation, use water at very high rates. In order to do this, these species must exist where there are quantities of water, and they must have root systems that are extensive enough to get at it. They usually occur along ravines, arroyos, streams, or rivers. Such species generally have more root material below ground than they have shoot material above. This arrangement is due to the fact that the plant's uptake of water is proportional to the amount of root material, and its loss of water is proportional to the amount of above-ground material. Many desert plants—not just water spenders—have nine times as much root material, by weight, as shoot material.

Phreatophytes have been a topic of controversy in the American Southwest. Because they take up so much water and simply "spend" it by way of transpiration into the air, some observers have believed that their presence along watercourses decreases the water available for human use. They have thus been regarded as pests that must be removed or controlled. The situation is a bit more complex, however. In general an area of land covered by phreatophytes loses less water than a site of equal size where they have been removed, because of the lower temperatures produced by the shading the plants provide. Furthermore, the organic matter produced by such plants increases the water-holding capacity of the soil, and the plants' presence helps prevent the runoff of rainfall. Such plants also provide excellent wildlife habitat in areas characteristically devoid of dense vegetation. On balance, phreatophytes would seem to be a positive presence, though they can be nuisances, as when you are trying to force your way through almost impenetrable stands.

Still other strategies of coping with the desert exist. Some species of perennials have the capacity to withstand drought by avoiding dehydration. These plants generally have small, deciduous leaves. When water is in short supply, they shed their leaves, reducing the surface area exposed to water loss. Certain of these species have green stems, branches, or trunks, and can carry on photosynthesis even without their leaves, in a manner parallel to that exhibited by the cacti. The palo verdes (*Cercidium*) are of this type. The translation of their common name, "green stick," alludes to their trunk color, which is imparted by the presence of chlorophyll. Palo verdes may produce forty percent of their annual food supply through stem photosynthesis.

Ocotillo
*Fouquieria splendens*
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Other plants that can avoid dehydration are the Ocotillo and its relatives. Like cacti, the Ocotillo has shallow, spreading root systems. During the dry season, its long, spiny stems are leafless. These spines actually develop from the midribs and petioles (stems) of the leaves. During wet periods, leaves develop along the whole wandlike axis of the stem. When several periods of rainfall occur, separated by drought, Ocotillo responds to each with a flush of leaves, which it subsequently sheds. Thus, on many Sonoran Desert sites, there are regularly two crops of leaves per year, coinciding with the biseasonal rainfall.

Most of these dehydration-avoiders close their stomates when even very slight water stress occurs. This closure, while preventing water loss, also prevents the exchange of gases. Thus, since these species cannot use CAM, as the cacti do, they cannot carry on photosynthesis. As a result, the plants begin to starve: Their leaves turn yellow, probably because they are moving nutrients out of their leaves into their stems as a conservation device. The leaves then die and drop off.

The last general group of species are termed the drought- and dehydration-tolerant species. These simply dry out. They manage to survive because their tissues can withstand drying without damage. Extreme examples from this category are lichens, mosses, and the Resurrection Plant. Some of these species can produce two very different types of leaves: one suited for moist periods, and another set that is better adapted to dry periods. The Brittlebush is capable of this, as are certain salt bushes (*Atriplex*) and Big Sagebrush. When water is particularly scarce, such plants may shed their leaves, though some, such as Creosote Bush, remain evergreen.

Brittlebush
*Encelia farinosa*
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Big Sagebrush
*Artemisia tridentata*
353, 357

The production of these different leaf types is quite complex. Leaves may differ in a number of ways, including size; pubescence, or hairiness; and thickness. Not all of these characteristics are equally affected by all environmental factors. For example, in Brittlebush at least, solar radiation primarily affects leaf thickness, while soil-water availability is a primary regulator of leaf length and growth rate.

Up to this point, I have ignored the biotic interactions of plants in deserts. Rather we have discussed the ways in which plants cope with the extremes of the desert's abiotic milieu. Here I turn to the biological interactions that represent responses to desert environments.

The spatial distribution of perennials follows various patterns. Broadly speaking there are three such general dispersion patterns. In the first one, each plant is roughly equidistant from every other plant; this is referred to as a regular dispersion pattern. Plants that follow this pattern to the extreme are spaced as equally as corn plants in a field or trees in an orchard. The second category consists of plants that follow a clumped dispersion pattern. These individuals grow close to each other in patches that are scattered across the landscape. In the third dispersion pattern, plants are distributed at random. This random dispersion pattern is not as likely to occur as the other two patterns, because organisms and their resources are not usually distributed at random in nature. An understanding of the reasons for these various patterns can reveal a great deal about the biology of the organisms involved.

The usual explanation for the regular dispersion pattern is that the organisms are competing for a resource such as water or nitrogen, and that each plant has defended its own living space. Experiments have shown that this is sometimes the case in deserts. The best example of this is probably Creosote Bush. These plants are thought to compete with one another for water. Since Creosote Bush is so long-lived, it may grow until its roots extend and interfere with the roots of another, adjacent Creosote Bush. This is in fact likely, because the roots of Creosote Bushes all eventually reach a similar depth, and horizontal spread of their roots is also similar.

In many areas of the desert, plants—including Creosote Bush—are not found in regular arrays. Instead they form clusters, arranging themselves according to the clumped dispersion pattern. It is believed that a particular resource that the plants require also has a clumped dispersion pattern, and that the plants can survive only where that resource is present. For example, they may cluster around a resource such as a localized zone of soil nitrogen, existing like a lens of nutrient material in the soil column. If the clump consists of a mixture of different species, the plants may be able to avoid competition: As long as each species has a different rooting strategy, it can obtain the resources it needs from a different soil level than the others do.

In each of North America's hot deserts, large complicated clusters of three to ten perennial species occur. These clusters have been best studied in the Mojave. In many places, annuals cluster under the cover of perennials.

Some clumped patterns are particularly interesting. Young Saguaro plants often grow under subtrees—especially beneath palo verdes. The young cactus benefits in several ways. It is shaded from intense sun and has available a good deal of organic matter derived from the litter collected under the palo verde. At the Saguaro's northern distributional limit, it may even gain some protection from freezing because of certain complex relations of radiation patterns. As the Saguaro grows, it begins to compete with the palo verde. The shallow, widely spread roots of the cactus intercept rainfall before it can percolate into the soil where the deeper palo verde roots occur. The palo verde, unable to acquire sufficient water, then dies, and the adult Saguaro survives. As palo verdes become established and grow on other sites nearby, Saguaros begin to germinate in their shade, and this long-term cycle repeats itself. The desert landscape is a rich mosaic of all the stages of this dynamic interaction.

Desert Christmas Cactus
*Opuntia leptocaulis*
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It has been suggested that a similar cyclical situation exists in the Chihuahuan Desert. Birds and mammals feed on the fruits of the Desert Christmas Cactus and deposit its seeds beneath Creosote Bushes. The cactus grows and its superficial root system begins to take up the water that the Creosote Bush needs. The Creosote Bush dies. Exposed, the cactus eventually succumbs to the influences of rodents and wind, and dies, leaving an open space that can be colonized by Creosote Bush—and the cycle begins again.

Joshua-tree
*Yucca brevifolia*
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Plants also interact with animals. On the positive side, there are a host of plant-pollinator interactions. The forty-odd species of the genus *Yucca*, for example, are all pollinated by three moth species in the genus *Tegeticula*. Of the desert yuccas, the Joshua-tree is pollinated by *T. synthetica*, while all others are pollinated by *T. yuccasella*.

The cycle begins when the female moth mates with the male moth inside a yucca flower. She gathers pollen from that flower, then speeds off to another plant and inadvertently fertilizes it. Her eggs are then laid in the ovary of the flower, and the larvae feed on the developing fruit, killing some—but not all—of the developing seeds. Ultimately the larvae leave the fruit and drop to the ground. In this complex relationship, the plant gets pollinated and the moth has a site and food for larval development.

Desert Willow
*Chilopsis linearis*
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Many other desert plants require insect pollinators, but not always in such a specific relationship. The Desert Willow can be pollinated by any of a number of bee species, whose common characteristic seems to be their large size. Although dozens of bees and beetles are known to pollinate cacti, the number of individuals of one species that you see visiting a flower doesn't attest to that species' importance as a pollinator. Some visitors are simply nectar thieves.

Vertebrates also pollinate some desert plants. Bats are known to pollinate agaves and Saguaros and hummingbirds pollinate red-flowered species such as Ocotillo.

Even though all of these examples of plant-animal pollination are interesting, deserts are prime areas for wind-based pollination as well, since they are open and windy. Many dominant desert species are wind-pollinated.



Pollination is not the only positive relationship existing between desert animals and plants. Seeds stored in soil caches by rodents are sometimes the ones most likely to germinate and become the next generation of plants. This has been observed in the Great Basin, where several rodent species store the seeds of Indian Ricegrass.

Indian Ricegrass
*Oryzopsis hymenoides*
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Buckthorn Cholla
*Opuntia acanthocarpa*

Animals can also protect plants from other animals. The Buckthorn Cholla produces nectar, not only in its flowers, but also within the developing tissue of new stems. This nectar attracts ants. One pugnacious ant species (*Crematogaster opuntiae*) attacks cactus-feeding insects in the Sonoran Desert and thus offers the plant a degree of biological protection.

Despite the many positive associations that exist between plants and animals, their roles are usually that of food and feeder. Many plants, however, have evolved mechanisms to prevent becoming food. Some build up chemical compounds in their leaves and stems that deter animals. In deserts a more obvious adaptation is the presence of spines, thorns, and prickles, which deflect herbivores.

If an animal removes a chunk of a plant, the plant suffers in two ways. First, the integrity of the plant's body surface is broken, and it may desiccate or become prone to disease attack. Second, since many resources, such as water, are not constantly available in deserts, a stem or a leaf cannot be replaced readily.

Interestingly, many of the browsers that may have prompted the evolution of spines—for example, the giant ground sloth of Pleistocene times—are extinct. Thus the presence of spines on desert plants today may be a result of interactions that occurred thousands of years ago, rather than one that we are likely to observe now.

There are thousands—even millions—of interactions between species that occur daily in deserts; biologists have not even begun to catalog them, to say nothing of understanding them. Any avid naturalist in the desert may happen onto one of these interesting relationships simply by sitting quietly and watching desert plants.

## Animals

Desert animals face the same problems as plants and often solve them in a similar manner. For example, the hairiness of some animals and the dense spininess or hairiness of some plants may reflect solar radiation, which would otherwise increase the organisms' body temperature. Similarly, thick layers of waxes or other material seal the water of plants or insects inside their bodies.

One striking difference does exist between the two groups: Animals are more mobile than plants and can often avoid environmental problems by moving away. Such avoidance adaptations take a variety of forms. On a daily basis, an animal may adjust the time of its activity to reduce exposure to environmental stress. Active only at night, nocturnal animals feed and seek mates during the coolest, most humid part of the day. Other animals are crepuscular—active at dawn and dusk. During these periods, there is more light, but favorable temperature and humidity conditions still persist. Animals can also avoid stress by migrating out of the desert during extreme periods, then returning during more hospitable times. Despite these vagility considerations, many animals stick it out; they have evolved morphological, physiological, and behavioral traits that are astonishingly diverse.

## Invertebrates Other Than Arthropods

Except for arthropods, which have impervious body coverings that resist water loss, invertebrates are not conspicuous in deserts. Some groups, such as snails, are abundant and conspicuous in some desert areas of the world, but are not nearly so obvious in the United States, though they may be observed locally. Minute forms such as protozoans undoubtedly occur as common elements of the soil fauna, but they have not been studied in detail, and thus we know little about their role in desert ecosystems or their adaptations, if any, to desert conditions. Their ability to form cysts, an encapsulated resting stage that may last for tens of years, makes them well-suited to desert environments, though this adaptation occurs wherever they exist and consequently is not really a desert-specific adaptation. Food sources such as bacteria and fungi, organisms that feed on plant residues, are periodically abundant in desert soils. We would expect then that periodically protozoans might also be common, and the few available studies suggest that they are.

Two groups of worms, the round worms (nematodes) and the segmented worms (annelids), have desert representatives. The most familiar annelids are the earthworms. Since earthworms require moist conditions, they rarely occur in the desert, except in sites such as riparian situations that are unusually high in soil moisture and organic matter.

A less familiar group of annelids, the enchytraeids, have been isolated in plant-litter samples retrieved from Chihuahuan Desert soils. They often feed on fungi, which, as we have noted above, are often abundant in desert soils.

Nematodes are as difficult to work with as enchytraeids. Luckily, however, scientists have expended considerable energy to find ways of studying them in desert soils. In general, they have found that nematodes occur in greater numbers beneath shrubs than in the open areas between shrubs. Also, their numbers decrease with depth. Thus, under a shrub in the Mojave Desert, there may be as many as 230 nematodes in a cubic inch of soil near the surface. The number drops to about sixty just ten inches below the surface, and to thirty or so in the surface soils between the plants.

Nematodes display a variety of feeding adaptations. Some species are fungus-feeding specialists, while others feed on microbes; still others are voracious predators or even parasites of plants. According to the available studies, microbe feeders predominate in desert soils.

Even though you could capture about one million nematodes



for each square yard of desert soil, not all of these individuals would be biologically active at any one instant. During unfavorable times, nematodes have the ability to go into a resting state, during which their metabolism is virtually unmeasurable. In essence the animals wrinkle up and dry out, but do not die. When water is again available, the nematodes "return to life." A great deal of variability exists in the spatial distribution of soil characteristics such as water content. This means that in one zone of a few cubic inches, there may be a veritable riot of nematode activity, while in an adjacent few cubic inches, all life may be in a resting state.

## Arthropods

The vast majority of conspicuous desert invertebrates are arthropods, which include wind or sun scorpions (solpugids), true scorpions, spiders, mites, insects, millipedes, centipedes, and even forms more generally thought to be aquatic, such as crustaceans.

Desert-avoidance adaptations are numerous in arthropods. Crustaceans such as fairy shrimp, clam shrimp, and tadpole shrimp, which inhabit playa lakes during periods of water sufficiency, undergo periods of inactivity, during which their development is arrested and their metabolism is diminished. This period of arrested metabolism is termed diapause. It can occur at almost any developmental stage, and it occurs widely within the phylum Arthropoda. When the proper environmental cues recur—especially the presence of water—these species commence development at a rapid rate and complete their life cycles in a short time.

A variety of insects and arachnids spend the hottest and driest portions of the day and year in burrows. Sometimes these burrows have been constructed by other animals, such as rodents. Other times, however, the arthropod must construct the burrow itself, which it usually does at the bases of plants. Here plant roots may have loosened the soil so that digging is easier. Additionally, plant roots reinforce loose soil so that tunnels do not collapse as easily. Digging species—certain scorpions, for example—may have enlarged palps or legs to aid in soil movement, while closely related species that merely retreat below surface cover do not show this development.

Some species adjust body temperature by moving deeper into the soil during the day. A good example of this behavioral thermoregulation is provided by nocturnal scorpions, which can essentially maintain low body temperature—even during the hottest portions of the day—by moving downward into their burrows. Despite this avoidance of high temperatures, scorpions can still endure very high body temperatures, even in excess of 115° F. Such temperatures are higher than those endured by most other arthropods.

On days when there is cloud cover, or cool air temperature, some predominantly nocturnal species can be seen on the surface during daylight hours. It is fascinating to explore the Sonoran Desert on a beautiful, cool, early spring day, as many animals that are nocturnal during the summer will appear.

Normally, day-active arthropods are not necessarily exposed to the high heat regimes that one might expect. Since these animals are small, their size alone offers them some advantages. First, the ratio of the animal's surface area to its volume is great, so that gained heat can be lost quickly. Of course the animals also heat up quickly. Second, and more important, these animals can fit into microenvironments that are much more favorable for them, a form of "escape" not available to a large species. An insect resting on a plant need only keep itself on the shady side of a slender stem or small leaf to reduce its heat load. Thus many day-active insects regulate their body temperature mainly by behavioral means. They expose their bodies to direct sunlight during the early morning to get their body temperatures up to optimum operating levels so that they can feed, fly, and mate. Then, as the daytime heat increases, they use shade-seeking behavior to avoid any further temperature increase. Even subtle changes in the angle of an insect's body to the rays of the sun can alter its body temperature. Thus, a grasshopper sitting on the open ground can lessen its heat load by resting with its body axis parallel to the sun's rays rather then perpendicular to them.

Some species actually manufacture their own shaded microsites. Several species of web-building spiders spin conical retreats that hang in their webs. Since these are placed in bushes—above the ground surface, where the temperatures are extraordinarily high—they are in relatively cooler air. The bush prevents reflections off of the ground from heating the cone's opening from below, and the white silk reflects the sun's rays from above. Such webs are built by common orb-web weavers of the genus *Metapeira* and by members of the single genus in the family Diguetidae, whose species are confined to the deserts of North and South America.

High temperatures are not the only problem a desert invertebrate must face. A cloudless night can cause the temperature to plunge, and so animals must also adapt to freezing conditions. In some invertebrates, body tissues are adapted to prevent damage even though freezing occurs. In addition, various "antifreeze" compounds may be present in some animals' body fluids. These compounds prevent freezing even when the animal's body temperature drops well below the freezing point of water.

If an arthropod must face harsh desert conditions, it must cope with or endure the environmental excesses. Once arthropods have taken up water, they dare not lose it. Water uptake can be accomplished in a number of ways. Species that feed on wet plant materials or on other animals may meet their water requirements by eating foods with a high moisture content. Other avenues of water uptake include the direct diffusion of water through the body surfaces by contact with free water, the ingestion of water by drinking, the production of water by metabolic activities, and the intake of water from the air. The availability of free water in a desert for either ingestion or uptake by diffusion seems at first to be at variance with the very nature of deserts. Remember, however, that at night



condensation can occur, and even small droplets of water that are of no use to large organisms are readily available to invertebrates.

More amazing is the fact that some species can actually extract water directly from air, even when the relative humidity is as low as fifty percent; more commonly they do so when the relative humidity ranges from eighty to ninety percent. Since water tends to move out of organisms in all but saturated air (one hundred percent relative humidity), this means that the animals are using some active chemical mechanism to harvest water from unsaturated air. This phenomenon has been especially well studied in a desert cockroach (*Arenivaga investigata*) that inhabits the Mojave and Sonoran deserts.

A final mode of obtaining water is to biochemically derive it from food. The biochemical breakdown of fat and carbohydrates produces water, and may be as important a water source for insects as it is for vertebrates.

Desert arthropods usually have mechanisms that allow them to resist desiccation rather than endure it. In contrast with plants, arthropods exhibit a quite limited range of variation in their tolerance to desiccation. An arthropod loses water in one of three ways: transpiration through its body surface; respiration; and excretory products.

Several cellular and noncellular layers help to seal the body surfaces of arthropods. Lipid compounds in the cuticle, chitin-protein complexes, and even the cell layers that produce these chemicals all help prevent water loss. Interestingly, the ability to prevent water loss may vary seasonally, and there is a concomitant seasonal change in the chemistry of body surfaces. In the winter, for example, tenebrionid beetles lose water rapidly. If, however, they are exposed to dry air, their cuticular chemistry changes and they reduce their rate of water loss. This form of physiological adjustment is termed acclimation. High temperatures can disorganize the molecular layers that prevent water loss, though usually these temperatures are so high (150° F) that if they occur, the animal would have succumbed to them for other reasons.

Although there are advantages to being small, disadvantages exist as well. There is proportionately more surface area that can lose water and a lesser volume of water to be lost in a small arthropod than in a large one. Some argue that this is the reason for the presence of large scorpions, spiders, and other arthropods in deserts, though this argument is not compelling when you observe similar animals in lush rain forests.

Excretion of both nitrogenous wastes and fecal material can use a lot of water. To prevent this source of loss, desert arthropods reabsorb water from feces in their gut tracts and thus deposit very dry fecal matter. Similarly, the water-wasting production of urine is a luxury a desert arthropod cannot afford, so insects produce uric acid, a dry nitrogenous form of waste, and scorpions and spiders produce the even more water-efficient compound, guanine.

Desert arthropods usually have low respiration rates, especially

since they may rest during drought periods. Both spiders and scorpions have amazingly low oxygen requirements. In France, scientists inactivated seven of eight of a scorpion's book lungs —specialized respiratory structures found in some invertebrates—and the remaining book lung was more than sufficient to meet all of the individual's respiratory needs.
Finally, the ability to endure the loss of a large percentage of body water without irrevocable damage is an important desert adaptation. Desert scorpions and spiders can easily withstand the loss of thirty percent of their body weight. In fact in one study, scorpions withstood forty percent body-weight loss with no serious consequences. This stands in sharp contrast with the lower tolerance for water loss found in their nondesert relatives.

## Fishes

Some desert sites in the United States contain permanent flowing or standing water. Fishes that inhabit such locales may not show much in the way of specialized adaptations to desert environments, because the physical and chemical conditions of these large water masses are stable and well within the normal limits of fish tolerances.
On the other hand, small streams or ponds may be subject to extreme daily and seasonal fluctuations of dissolved oxygen, temperature, and salinity. Under such conditions, specialized adaptations are required to ensure the survival of the fish population. Desert fishes must endure low quantities of oxygen dissolved in their water. In fact, North American desert pupfishes (*Cyprinodon*) have survived at the lowest oxygen concentrations known for any fish, that is at one fiftieth to one seventieth of the level present in normal water.
In deserts in other parts of the world, certain fishes can occur in ephemeral ponds or streams. They do this by producing eggs, which, like the seeds of annual plants, survive when the adults die off as the pond or stream bottom becomes dry soil. Alternately, adults may survive in moist to dry sediments in a state of aestivation. No desert fishes in the United States can do this. The only species that comes close is the Longfin Dace, which can survive for at least a day under water-saturated mats of algae and debris in Sycamore Creek in Arizona.

Longfin Dace
*Agosia chrysogaster*
296

In the United States, most desert fish live in essentially permanent ponds or streams. The minnow family (Cyprinidae) and the sucker family (Catostomidae) are stream forms, while the tooth carp (Cyprinodontidae) and the live bearers (Poecilidae) are spring or pond forms.
Interestingly, these desert fishes are in great peril. Of the approximately thirty-one North American fish species that are endangered, twenty-three occur in the deserts of the southwestern United States. This danger stems, in part, from the introduction of non-native species such as the Golden Shiner, the Mosquitofish, bass, and others that compete with, consume, or otherwise interfere with the native populations.

Golden Shiner
*Notemigonus chrysoleucas*
299

Mosquitofish
*Gambusia affinis*
294

The precarious status of some of these populations is also related to the fact that most species live in habitats that are physically small, which makes these habitats much more susceptible to catastrophic disturbance due to irrigation and other human activities.
Despite their sensitivity to the altered biological milieu within their habitats, American desert fishes exemplify the extremes of physiological adaptations to deserts. For example, pupfishes can withstand temperatures that range from 34° to 112° F, even though successful reproduction can only be accomplished within the much narrower temperature range of 75° to 86° F. At higher or lower temperatures, the female is unable to produce eggs.
Like insects, desert fishes employ behavioral thermoregulation. In the morning, they leave the cooler water of spring-fed ponds or streams and spend the day feeding in water that is within three to five degrees of their upper thermal-tolerance limit. They live life at the edge of their upper limit because high temperatures permit the fish's biochemical system to work optimally while the animal feeds. The lower nighttime temperatures are adequate for the fish's normal resting requirements.
In addition to broad thermal ranges and low quantities of dissolved oxygen, the desert fishes must endure wide fluctuations in salinity. As water evaporates from streams and ponds, the salt concentration can increase to a level equal to three to five times that of seawater. Water in solutions that are separated by membranes moves across these membranes in response to the concentrations of salts on either side of the membranes, a process termed osmosis. Thus the cells of fish, which are obviously surrounded by membranes, gain or lose water in response to the concentration of the water in which they live. When their environment has a higher salt concentration than their cells, they lose water. Conversely, when their cells have a higher concentration than their environment, they take up water by osmosis. The fluids in the bodies of fish contain about fifteen parts per thousand of salt. In fresh water, because of their high salt concentrations, these fish can simply take up water through their body surfaces. In seawater, however, which is about thirty-five parts per thousand of salt, water tends to leave the fish's body. Therefore the fish must drink salt water and retain the water but excrete the salts—both via the kidneys and, especially, through the gills. In a desert spring, where the water is commonly two and a half times as salty as seawater (eighty-eight parts per thousand) and is occasionally five times as salty (175 parts per thousand), fish are under almost constant physiological stress. Efficient excretory mechanisms permit survival.
These remarkable fish deserve our protection. Anything that can survive in such a harsh natural environment should be revered, not extirpated by humans through the destruction of its limited habitats and the introduction of an alien fauna.

## Amphibians and Reptiles

Amphibians require moist places for breeding, with most species needing the water of a pond or a stream, or at the very least, moist soil. Because their skins are moist and lose water rapidly, the adults generally must also have a moist substrate to replenish their body water. In addition, the vast majority of amphibians are not very tolerant of salt. All of these requirements are in stark contrast with typical desert conditions, so it is no surprise that very few species of amphibians have adapted to these environments. Only one North American species of salamander, the Tiger Salamander, occurs regularly in deserts, principally in the Chihuahuan. The Tiger Salamander is opportunistic and survives under locally favorable conditions. Since such favorable sites occur sporadically over a wide geographic area, this species appears in a number of desert localities. A few other salamanders live in canyons that extend into the desert, and thus might be encountered in a desert area.

Tiger Salamander
*Ambystoma tigrinum*
289, 290, 291

In general, frogs are the only amphibian denizens of the desert. And among frogs, only two families—the spadefoots (Pelobatidae) and the toads (Bufonidae)—make up the overwhelming majority of amphibians you are likely to see amidst true desert conditions in the United States.

True frogs, or the family Ranidae—one typical species is the Northern Leopard Frog—are often found in deserts, but they are associated with permanent water. The story is the same for "desert" treefrogs, such as the Canyon Treefrog and even for some toads. The Southwestern Toad occurs in isolated populations that are scattered around the Southwest. Many of these areas have been irrigated for thousands of years, from the times of prehistoric cultures to the present; this habitual irrigation may have permitted this toad to persist in desert situations. The Colorado River Toad is another toad with similar requirements: It is semiaquatic and must have permanent water. All of these frog species avoid the water problems of the desert by finding a consistent source of available water.

Northern Leopard Frog
*Rana pipiens*
286

Canyon Treefrog
*Hyla arenicolor*
272

Southwestern Toad
*Bufo microscaphus*
279

Colorado River Toad
*Bufo alvarius*
281

Some toads and spadefoots, on the other hand, show remarkable adaptations to desert conditions. Many species have no definite breeding season—these animals can respond instantly to the availability of water and commence the process of reproduction. This differs from the behavior of species with well-defined breeding periods, which are often regulated, in part, by such seasonal environmental factors as the length of the day. In these latter cases, when the proper day length exists, the frogs are physiologically able to breed; however, they cannot breed either before or after that time, regardless of other environmental conditions. The disadvantage of this restriction in a desert is obvious. If day length is correct, but no rain falls, the frog cannot successfully produce offspring. Similarly, if rain occurs but day length is incorrect, the frog will again fail to breed. The most limiting and unpredictable factor, water, must be the ultimate cue to begin reproduction. This allows the desert-adapted frog to use even very temporarily available water.

The presence of loud voices in male desert frogs is thought to



be an adaptation to bring males and females together, quickly, at the site of temporary water. When the eggs are laid, they develop rapidly, as do the tadpoles. This permits these species to avoid desiccation as the water body shrinks. Sources of food may be scarce in a temporary pool, so a desert tadpole, instead of being an herbivore like the tadpoles of most frog species, must be omnivorous, consuming both animal and plant matter. In extreme situations, when resources are limited, tadpoles may even become cannibalistic. Since the temporary water is often exposed to direct sunlight during the day, tadpoles must have a tolerance to high temperatures. Indeed many species can endure temperatures of over 100° F.

For adults, "avoiding" desert conditions is important. During most days, and constantly during dry periods, adults must burrow to keep moist and to avoid high temperatures. To do this, the hind foot of many species has a horny, bladelike structure to loosen and dig into the soil. These spades are quite conspicuous because of their dark color in spadefoots (*Scaphiopus*)—named for this adaptation—and some toads, such as the Great Plains Toad. These frogs are active on the surface most typically at night, when drying conditions are minimal.

Great Plains Toad
*Bufo cognatus*
283

Nevertheless, adults, despite their best efforts to avoid drying conditions, will inevitably begin to lose body water. It is important that they be able to withstand some loss without being incapacitated—and thus becoming easy prey. In fact desert frogs can survive body-water losses of up to fifty percent of their body weight.

Couch's Spadefoot
*Scaphiopus couchi*
274

Couch's Spadefoot is probably the most highly adapted to deserts of any of the American frogs. Using its spade, Couch's Spadefoot constructs burrows twenty to twenty-five inches below the soil surface, usually in close proximity to a plant, especially a shrub. Here it may remain dormant for more than two years. To prevent water loss under these conditions, the Spadefoot has several adaptations. The first, a morphological adaptation, is the Spadefoot's ability to encase itself within a dry, hard covering. Careful inspection shows that this covering is composed of several layers of skin that have been shed from the body surface, but which remain to surround the frog as a protective cocoon.

Buried in this way, the animal has a tendency to lose water more slowly, but it still loses water where its wet body touches dry soil. In this circumstance, certain physiological adaptations are helpful. As the soil continues to dry, the Spadefoot accumulates urea—the compound found in urine—in its tissues. This concentrates the Spadefoot's body fluid and slows the loss of water. In addition, before they begin to burrow, Spadefoots accumulate very dilute urine in their bladders. This adaptation allows them to accumulate an amount of water equal to thirty percent of their body weight to use as needed. To endure the extreme chemical changes occurring in their body fluids, the muscles of the Spadefoot are able to tolerate a much higher urea concentration than can those in most other vertebrates. Stored fat is used to fuel the

Spadefoot's very low rate of metabolism during this phase. As water is lost, the Spadefoot's tissues endure the drying, up to the point of losing fifty percent or more of their weight. When the rains come and the toad digs its way to the surface, it quickly replenishes its body water merely by being stationary. There is a patch of thin, highly veined skin on the abdomen between the hind legs. This "sitting spot," equivalent to perhaps ten percent of the body area, may absorb up to seventy percent of the water taken up through the body surfaces.

Once on the surface, males make their way to a temporary body of water, where they utter breeding calls that can be heard literally for miles across the desert.

Breeding is accomplished rapidly. Usually the adults are out of the ponds within three to five days, with most breeding having occurred on the first two nights. The freshly laid eggs are not as tolerant of high temperatures as later embryonic stages are, but their development is so fast that within ten hours—by morning—they can withstand temperatures in excess of 100° F for two-hour periods. By the time the eggs are thirteen hours old, they have hatched into tadpoles. The same progression may take many days in other frogs. In just seven to ten days from the moment of fertilization, the cycle is complete, and small Spadefoots are ready to emerge from the ponds. In the northeastern United States the same process may require a period of months, and over a year for certain species.

The upshot of its adaptations is that the Spadefoot can maintain large, viable populations in many areas that seem quite unfit for habitation, for months or even years at a time.

The evolutionary jump from amphibians to reptiles included, among other things, the development of adaptations to a terrestrial environment. A better skeletal system to support a body not buoyed up by water, a covering of scales to reduce the rate of water loss, and a shelled egg that did not have to be placed in water were three of the prominent developments. It is not surprising, then, that reptiles are better adapted to deserts, the most extreme of terrestrial environments, than are the amphibians.

For reptiles there are three major sources for the gain or loss of heat. Heat can be conducted to or from the air; it can be conducted to or from the ground or any substrate upon which the reptile lies; and, finally, of course, heat is conducted by radiation from the sun. Reptiles, like amphibians, regulate their body temperatures mainly by gaining heat from their environment in these three ways. The amount of heat produced by their own metabolic processes is a very small portion of the heat required to maintain their body temperatures. They are thus called ectotherms—a word denoting creatures that use outside thermal sources to maintain body temperature. By contrast, birds and mammals have very high metabolic rates and are very well insulated by their body coverings of feathers or fur. Their body temperatures are regulated by using metabolic heat from internal sources, and they are termed endotherms.



This difference between ectotherms and endotherms has important consequences in the desert. When animals breathe to meet their metabolic demands for oxygen, they also lose water from their lungs. A lizard of the same body mass as a rodent has one-seventh the mammal's metabolic rate at 100° F; thus it breathes less often and conserves water.

To regulate its body temperature, a lizard or a snake crawls out of its overnight refuge and exposes its body to the sun. It gains heat from the warm soil, from the air, and directly from the sun's radiation. When its internal body temperature is at an optimum level, the reptile attempts to prevent the gain or loss of additional heat. This can be accomplished in several ways. If too hot, for example, it may move to the cover of a shaded bush. There the sun is no longer heating it up, and in the cool shade, heat loss can take place as well. The heat from the soil can be avoided by lifting the body off the surface: There is less body-surface area in contact, and thus less heat is gained. Some lizards avoid contact with the ground by running only on their hind legs, keeping the front part of the body off the soil surface.

Desert Iguana
*Dipsosaurus dorsalis*
188

Some species, such as the Desert Iguana, employ the opposite technique: They hug the ground. In such cases, the lizard actually pushes aside the hot surface soil and puts its belly in contact with the cooler subsurface soil, thus losing heat by conduction.

Even the position of a reptile makes a difference in its body temperature. If it places its body perpendicular to the sun's rays, it will absorb the greatest amount of heat. If it turns ninety degrees, parallel to the sun's rays, it can minimize its absorption of radiant energy. Additionally, changes in color affect temperature. A dark lizard absorbs sunlight; a lighter one reflects more sunlight and thus heats up less. The skin of desert lizards may reflect thirty-five percent of the radiation falling on them, in contrast with about six percent for tropical species.

The scales of reptiles can also influence their thermal relations. Rough scales may form air spaces, which have the effect of insulating the animal to some extent. On the other hand, scales like these may prevent water loss—and also evaporative cooling—under circumstances when water loss is called for.

Thus a hot lizard or snake that cannot control its temperature by its position within the environment must pant. It cannot sweat. Panting provides the cooling effects that occur when water evaporates from the lungs, and thus lowers the body temperature. A lizard that respires nineteen times per minute at 104° F may pant fifty-nine times a minute at 110°, a temperature close to its lethal upper limit.

Different species can withstand different body temperatures. For reptiles in general, active body temperatures fall in the range of 88–102° F, with a mean of about 95°. The highest body temperature at which an animal is voluntarily active seems to be that of the Desert Iguana, which is regularly active at 115°, a value quite close to its lethal temperature of about 118°.

The lethal temperatures of snakes are lower than those of lizards. This may in part explain why most desert snakes are nocturnal, avoiding the heat, while most lizards are diurnal.

Sidewinder
*Crotalus cerastes*
252, 253

Coachwhip
*Masticophis flagellum*
223, 224, 227, 229

The nocturnal Sidewinder often lives in the same places as the diurnal Desert Iguana. Its lethal temperature of about 105° F is thirteen degrees lower than that of the Desert Iguana. Even the diurnal Coachwhip can withstand only about 111° F and is usually active at body temperatures of less than 95° F.

Desert reptiles cannot obtain water through their skins as easily as the amphibians can. Their protective scales prevent not only water loss, but water uptake as well. Reptiles in deserts usually do not have the opportunity to drink, though some species may use dew. The result is that food is the principal means of water uptake for most species. In fact desert reptiles generally cannot exist on food with a water content of less than sixty percent.

Chuckwalla
*Sauromalus obesus*
189

Most reptiles—and all amphibians—are carnivores. Thus their water-uptake problems are solved by eating moist prey. For the few herbivorous reptiles, plant material may provide water, but there is frequently an associated problem. Desert plants often contain high salt concentrations. This extra salt is lost by most reptiles in their fecal matter, but nasal passages in some lizards, including the Desert Iguana and the Chuckwalla, contain salt-secreting glands that aid in maintaining the correct concentration of salt in their body fluids.

Of the water lost by reptiles, thirty to forty percent is lost through their feces—though these are relatively dry and contain nitrogenous body wastes in the form of dry uric acid. The remaining sixty percent or so of the body water is lost equally via respiration and through the skin.

Some species can lose water until they have lost fifty percent of their body weight—a high tolerance. Certain reptiles, such as Desert Tortoises, actually store water in their bladders.

Fringe-toed Lizard
*Uma notata*
182

Reptiles deal with loose substrates in a variety of ways. Fringe-toed Lizards, which are confined to sandy areas, have fringed scales on their toes to permit running across the sand. The scales operate somewhat like snowshoes, dissipating the animal's weight over a larger area of the sand. To prevent sand from getting into its nose, the Fringe-toed Lizard has closing valves, and its lower jaw is overhung by the upper, which keeps its mouth sandless. Its flat body and smooth scales minimize friction, allowing it to "swim" through the sand.

A few snakes, such as the shovelnose snakes (*Chionactis*), have similar mouth, nose, and scale adaptations. In addition, when such a snake comes to rest beneath the sand, it bends its head downward, leaving a space beneath its throat. In this small space, the snake can pump the muscles of its throat, bellows-fashion, pulling air from between the sand grains. It may be that many desert snakes and lizards with pushed-up or hooked noses use these to hold their heads at an angle in order to produce the same type of space beneath their necks.

A unique form of locomotion, sidewinding, is another adaptation to loose substrates. The J-shaped tracks resulting



from this serpentine movement are caused by the animal throwing a loop of its body forward rather than sliding the whole body along an undulating, continuous pathway. This strategy prevents sideslipping, and increases efficiency of movement.

It is clear that reptiles, through a myriad of adaptations, have come to terms with the desert. Their abundance as you walk the deserts, day or night, attest to their success. Careful observation will allow you to see that the repertoire of behaviors of desert animals is not a series of random happenings, but is rather a highly orchestrated program, adapting the animal to a harsh and unpredictable environment.

## Birds

Bird species are not numerous in North American deserts, compared with other habitats. Those that do occur in deserts frequently do not exhibit unique morphological or physiological adaptations to desert environments. This is partly because, due to their flight ability, birds are so vagile that they can travel several miles to sources of water and fly up to high altitudes, where the air can cool them and they can escape the rigors of the desert. In sharp contrast, small mammals are, over the course of a day, essentially confined to a narrow environmental zone, which extends from the vegetation a few feet above ground to burrows a few feet below. This zone covers an area that is generally much less than a mile in diameter, and quite often less than a few hundred feet. Nonetheless birds do have some adaptations to dryness and heat that suit them to a desert existence.

Birds have higher normal body temperatures than most other vertebrates; these often exceed 104° F. Obviously, they do not have to cool their bodies in response to the air temperature until the air temperature exceeds that of their bodies. Since cooling often involves the loss of water by evaporation, birds are better off than mammals, whose normal body temperatures are closer to 99° F, and who must thus cool themselves at lower air temperatures. Additionally, birds may allow their body temperatures to rise an additional 5° or 6° F, putting off the need to cool themselves until the environmental temperature reaches 110°, a condition that seldom occurs in the shade of plants, even those that form a very loose, open canopy, such as desert subtrees. There is a limit to this, however: Few birds can endure a body temperature in excess of 115°. In part, the mechanism for heat loss from birds when they are warmer than the air involves direct radiation of body heat to areas of lower temperature. This direct radiation does not involve the water loss of evaporative cooling.

Behaviorally, birds avoid the thermal problems of the desert day by confining their activities to the cool early morning and, to a lesser extent, to the late afternoon. During the warm periods, most species rest in the shade of vegetation or rocks. Since flying may increase body temperature, some birds may not be able to fly during the desert day, because the combination of their metabolic heat and that of the air might cause their body temperatures to exceed their thermal limits. As alluded to earlier, high-flying birds can be active during the day because they are flying in air of lower temperature than are their kin close to the ground.

The position of the feathers when the bird is at rest can contribute to cooling. Some feathers are compressed. This destroys the insulating air space between the feathers and the body surface, and allows heat loss. Extending or raising the wings exposes lightly feathered areas along the sides of the body. Such positions increase heat loss, much as does raising your arms on a hot day.

Lesser Nighthawk
*Chordeiles acutipennis*
560

Roadrunner
*Geococcyx californicus*
554

If all of these methods of heat loss prove to be insufficient, birds use evaporative cooling. Panting through the mouth is the main avenue for the evaporative water loss; however, some species, such as the Lesser Nighthawk and the Greater Roadrunner, use their throat muscles to pump air in a process called gular fluttering. Gular fluttering is metabolically less costly than panting.

Black-throated Sparrow
*Amphispiza bilineata*
610

Regardless of whether a bird loses its body water to general evaporation or to evaporative cooling, the water must be replenished. Three sources of water are available. As birds metabolically oxidize food that contains hydrogen, some water is produced, though this is a very minor portion of the water they require. Water that is preformed in food—that is, it exists in the food as water and does not have to be chemically manufactured—is another, more important source. Black-throated Sparrows, among the most desert-adapted American birds, can survive using only preformed water if sufficient green plant matter or insects are available. Perhaps most of the birds that feed on animals, nectar, and fruit find sufficient water in their normal food to survive, while seedeaters may generally have to augment their diet. Few birds in the world feed entirely on green matter, so succulent leaves are not a common source of water.

Finally, the most important water is free water, that which is available for drinking. Many seed-eating birds flock to water holes to drink, even though they must sometimes travel many miles to do so. Bird-flock movement can provide a stranded traveler with a clue as to the whereabouts of free water.

Birds are not well adapted to drinking salt water. Their kidneys are not as efficient as those of mammals, because they are structurally less well developed. Thus they cannot conserve the water or excrete the salts from salty water sources. Some marine species have salt-secreting glands in their nasal passages, but most desert species do not. An exception in the United States is the Roadrunner. However, the function of its salt gland seems to be unrelated to drinking salty water. Rather, because nestlings lose water by evaporation, the only way to keep their fluid concentration within the correct range is to excrete salt via the nasal glands. The bottom line is that, as far as we now know, desert birds can make only limited use of saline water as a source of drinking water.

Water-conserving adaptations occur in birds as they do in most desert animals. The nitrogenous waste product of birds is uric acid, which does not dissolve well in water and which is excreted in a dry, semisolid form. This conserves a great deal of water, considering the amount that goes into the watery urine of mammals.

Birds do not have sweat glands. This lack is an adaptation to flight, but it also reduces evaporative loss through the body surface. Nonetheless, their small body size and the consequent high proportion of body surface area causes birds to lose water through this avenue, especially during exercise such as running or flying.

Cactus Wren
*Campylorhynchus brunneicapillus*
584

Losses from the nasal passages are reduced in some species by a unique pattern of condensation. Birds lower the temperatures of their nasal passages so that as warm, expired air passes from the lungs through this zone, condensation occurs, and this condensed water is recaptured. The Cactus Wren is known to recover up to three-quarters of the water from its expired air in this manner.

The water that would ordinarily be lost in feces is resorbed in the gut tracts of birds. There is some indication that this is done more efficiently in arid-land species than in those of humid areas.

House Finch
*Carpodacus mexicanus*
617, 618

It is not clear that desert birds can tolerate a greater degree of water loss than nondesert species. In part this is because there is so much variation among birds in general with respect to how much water loss they can withstand. Desert species range in tolerance from the House Finch, which can survive the loss of up to twenty-six percent of its body weight, to certain quails that can withstand water losses equaling fifty percent of their body weight.

Violet-green Swallow
*Tachycineta thalassina*
579

White-throated Swift
*Aeronautes saxatalis*

Common Poorwill
*Phalaenoptilus nuttallii*
562

There are other problems in deserts besides heat and dryness. Bouts of cold can catch year-round residents without enough food to meet their daily energy requirements. Mammals avoid these conditions by going into torpor, a resting state not possible for most birds. In American deserts, however, several birds use torpor to avoid cold conditions. Species saving their energy in this way include the Lesser Nighthawk, the Violet-green Swallow, the White-throated Swift, and the Common Poorwill. Birds adjust to the desert in a variety of other ways. Domed nests protect some species. Regulation of the breeding season to coincide with the periodic availability of food is an adaptation to desert irregularity.

However, these and all of the physiological adaptations we have discussed occur to some degree in nondesert birds, often to nearly the same extent. Clearly, while some birds inhabit deserts, they are not the favored spots of the vast majority of species in the United States during the hottest, driest portion of the year.

## Mammals

Mammals—especially rodents of the family Heteromyidae—are common and, at least at night, conspicuous components of desert ecosystems in North America. The small size, nocturnal habits, and seed-based diet of these rodents form a suite of adaptations that permit them to persist in the face of the high heat and the low, irregular availability of water. There are several other ways to cope with the same environmental conditions, however. Thus some mammals are large rather than small, some are active diurnally rather than nocturnally, and not all desert mammals specialize in eating seeds. We shall consider several of these contrasting strategies and their relative advantages as we dissect the complexities of mammalian adaptations to deserts.

Response to high temperatures usually involves sweating or panting. While large desert mammals may employ these two modes of evaporative cooling, rodent-size mammals do not. In rodents higher temperatures do not induce the increased respiratory rates characteristic of panting, and rodents do not have sweat glands, although they do lose water through the body surface and in expired respiratory "air." As a result, their main relief from thermal stress is to escape to a more favorable thermal environment. There is, however, one interesting cooling method used by a number of species when they are under thermal stress: They lick their fur. This water evaporates and cools the body surface, yet it requires a lower energy output than panting.

Burrowing and being nocturnal are the main methods by which small desert mammals avoid thermal problems. The temperature of a burrow that is as shallow as eighteen inches below the surface does not vary more than two degrees in the course of a day and, even during the hottest portion of the year, probably never exceeds 85–90° F. This constancy contrasts with the temperature of the soil surface, which may heat to 170° during a day with air temperatures of 105°. At night the heat of the ground surface is rapidly radiated to the clear sky. This can cause the temperature of the soil surface to fall below the air temperature, and to be as much as ninety degrees cooler than the daytime soil temperature. While many mammals simply remain in burrows until nightfall, ground squirrels (*Spermophilus* and *Ammospermophilus*) are active during the day. These animals can feed until their body temperatures increase. Then, by running down their burrows and hugging the substrate, they lose the accumulated heat, by conduction, to the cooler burrow. Once they have cooled off, they return to the surface for another cycle of foraging followed by burrow entry and heat loss.

Black-tailed Jack Rabbit
*Lepus californicus*
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Larger mammals, such as the Black-tailed Jack Rabbit, do not usually burrow, and so must seek the shade of rocks or vegetation to keep cool. In very hot weather, however, an individual may dig a hole that completely conceals it, but this does not comprise an elaborate tunnel system. The large surface area and high vascularity of the Jack Rabbit's ears allows the ears to act as radiators, losing heat to areas of lower temperature, especially the sky. Unlike the smaller rodents, Jack Rabbits "pant" through their noses and use this action as a form of evaporative cooling. Since they are herbivores and favor succulent vegetation, they replenish their water from preformed water in their food. In the hottest portions of the



day, these rabbits may allow their body temperatures to increase very slightly.

Mammals that are even larger than the rabbits gain some thermal advantages in deserts because of their body size alone. First, large animals are generally more mobile than small species. They can travel great distances to permanent water such as isolated springs or temporary pools in watercourses. Thus they do not depend on metabolic and preformed water from their food alone, and they can afford the luxury of evaporative cooling for some part of their thermal regulation. The large body size also reduces the surfaces that are exposed to heating in proportion to the mass of the body. This resistance to heating is further augmented by the thick, insulating fur of larger mammals. Another consequence of large body size is that, because of their mass alone, their body temperatures increase more slowly than those of smaller animals. This is because tremendous heat is required to raise the temperature of an ounce of water, and large animals have many more ounces of water than their diminutive relatives. Thus they can accumulate heat during the day and lose this thermal load either at night by radiation or during the day by retiring to shade.

Merriam's Kangaroo Rat
*Dipodomys merriami*
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Problems of water conservation are solved by mammals in a number of ways, but perhaps the most significant adaptations are those related to kidney function. Small rodents such as Merriam's Kangaroo Rat can produce urine that is so concentrated that it crystalizes as soon as it is passed from the body. Such a concentration is five times that of the most concentrated urine that human beings can produce. This is accomplished through a complex series of morphological and physiological adaptations of the kidney. One of the more easily understood is that the tubules in the kidney, which are used to reabsorb water before urination takes place, are longer in desert mammals than in nondesert species and therefore recapture more of the water. Similarly, rodents can drink saline water, as their kidneys can extract the water and excrete the salts.

Dry feces are also produced by small desert mammals to aid in water retention, and even the shape of the nasal passages in many species conserves water from expired air by condensing and absorbing the water before exhalation occurs.

Many desert heteromyids have metabolic rates that are lower than those of nondesert rodents of similar size. Lower metabolic rates conserve energy and, consequently, the loss of water. A further metabolic adaptation of some heteromyids is the ability to enter a state of torpor, during which time body temperatures and energy metabolism are decreased. This state can be entered daily or for a longer term. Torpor is an energy-conserving adaptation used by any heteromyids that are less than about forty grams in weight. This weight represents the size break between the small pocket mouse (*Perognathus*) or kangaroo mouse (*Microdipodops*) species, and the larger kangaroo rats (*Dipodomys*). Small kangaroo rats—for example, the thirty-five-gram Merriam's Kangaroo Rat—can go into a

Round-tailed Ground Squirrel
*Spermophilus tereticaudus*
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torpor induced by cold or starvation, but it lasts for short periods and occasionally results in death. Some nonheteromyid rodents, such as the Round-tailed Ground Squirrel, exceed the forty-gram torpor boundary, but nonetheless effectively use torpor to conserve water and energy.

In some species, such as heteromyids, the combination of efficient kidneys, nocturnal habits, and highly adapted nasal passages, among other adaptations, permits them to exist on only the water found in dry seeds. Thus these species are completely independent of the need to drink. It should be noted that "dry" seeds contain a considerable amount of preformed water, perhaps up to twenty percent by weight when they are stored in the relatively high humidity of burrows.

Many small desert mammals are bipedal—that is, they run on their hind feet, which are often enlarged compared with those of other mammals of similar size. There are many possible interpretations of the adaptiveness of this condition, but the most reasonable seems to be that bipedality permits fast, erratic, balanced movement, an aid to avoiding predators in open habitats. Additionally, kangaroo rats and, to a lesser extent, pocket mice, have bulges on the back and side portions of their heads. These enlarged skull areas are related to the middle-ear chamber; through a complex series of relationships, they permit animals to detect low-frequency sounds. This detection process is effective in determining the presence of predators in the dim light that often exists at night when heteromyids are foraging.

Much has been made of the color of desert animals. Some observers have argued that coloration is more important in determining thermal balance than any other function. The presence of many black desert animals does not seem to agree that this is the most plausible explanation. Other suggestions have been advanced, but the result of all of these cerebrations is neither clear nor compelling. However, the general thesis is that most color patterns are meant either to conceal animals or, quite to the contrary, to advertise an organism's presence because it is toxic. For mammals, the cryptic-coloration hypothesis seems an adequate explanation for the North American species.

Most medium-size mammals—such as foxes, Badgers, and Coyotes—are nocturnal carnivores. As such, these species get water from their food, and they avoid the heat and drying air of the daylight hours. This combination avoids the problems of the desert just as effectively as the more complex adaptations of some of the smaller species.

Many mammals are adapted to the rigors of the desert environment. Some families are especially finely tuned—both physiologically and morphologically—to deserts. In North America, the heteromyid rodents, the most characteristic desert mammals, are a good example of animals that exhibit a plethora of such adaptations. You need only follow a kangaroo rat for an evening in the light of a flashlight to gain a sense of awe for these desert specialists.