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CHAPTER THREE

The Biological Richness of Deserts

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A desert is "waterless," "treeless," "barren," "remote," "uninteresting," and "presumably uninhabited," according to the authoritative Oxford English Dictionary. The word is derived from *deserere,* a Latin verb meaning "to leave." In English, *to desert* is still to "abandon," "forsake," or "fail." Because language shapes perception, emptiness tends to figure prominently in one's first (and possibly lasting) impression of any place referred to as a desert. What *should* be there (water, trees) is absent. What *is* there is useless and dull. "Normal" plants and animals may once have lived there, but if so, they found the place inhospitable and eventually departed, leaving behind an impoverished residue of twisted, spiny losers.

This negative view of deserts is widely held and frequently reinforced. It is also very inaccurate. Like many stereotypes, it may have caused little harm when the object of the stereotype really *was* remote. But no place is remote any longer, and deserts are increasingly subject to many kinds of large-scale human disturbances. What we do to deserts is determined in large part by our attitudes toward them, and these attitudes are shaped in powerful ways by what we *see* in deserts—quite literally, by what we think they consist of and how we think they work.

In this chapter we attempt both to expose and to refute the conventional stereotype of deserts as wastelands. We then describe the enormous economic, ecological, scientific, educational, and recreational values of deserts. Finally we argue that informed and far-sighted management practices must be developed if these values are to be preserved. In many cases all of these values will either be preserved or lost together.

The Stereotype: Barren, Boring Barriers

Why do deserts get such bad press? The answer is in part historical. During the nineteenth century, when the American West was being colonized, no community could exist without a local agricultural base. Deserts are generally not suited to agriculture, particularly in the absence of mechanized irrigation. Thus the deserts of Western North America were inevitably perceived as little more than obstacles on the way to California. The pioneers needed to find the flattest routes for their wagons; these are generally the lowest, and therefore the hottest and driest. Many of our modern highways take these same traditional routes, or ones of similar character. Along these routes the mountains continue to serve mainly as visual backdrops, and they remain largely unexperienced. Even worse, people tend to travel (now as then) in the summer and during the day, when many plants and animals are relatively inactive. No doubt the early travelers often noticed what happens at dawn, dusk, and during the night, since they slept out of doors. But modern travelers usually stay in air-conditioned motels, insulated from the life that may appear just a few yards away when the sun goes down.

Many early travelers in the West marveled at its spectacular geology, but to most even the geology must have seemed alien and forbidding. Compared to mountains in the East, those in the West were unnaturally large, rough, and exposed. A hot, tired, and anxious traveler could hardly have been in a frame of mind to appreciate rocks whose endless diversity, overwhelming the mind's capacity for appreciation, would have come to seem yet another reminder that the long journey was still far from over. Also, the young mountains of the arid West are very obviously being *eroded*. An image of *removal* has therefore been associated with *aridity* in the experience of generations of Americans. To this day the term "desertification" is used to describe any situation in which erosion of soil severely limits plant cover. This usage gives the word "desert" the additional (and unwarranted) negative connotations of "attrition" and "destruction."

From the Old Testament to the latest screenplays, writers have found in deserts a powerful symbol of struggle against the elements, in a setting of supreme isolation. They therefore tend to emphasize the harshest, least inviting aspects of the stereotype. The desert stands for obstacles (both external and internal) that the hero must conquer—adversity from which he (seldom she) must wrest a victory that will come hard, if it comes at all. Sand dunes are the icon, and what they stand for is absolute desolation.

What's Wrong with This Picture?

In a word, everything. For example, typical sand dunes are far from Saharan. Contrary to the stereotype (and seemingly to common sense), dunes are among the most productive of desert environments, and they often have remarkably high diversities of plant and animal species. (There are more than 50 species of plants at Coral Pink Sand Dunes in Utah, around 60 on the gypsum dunes at White Sands National Monument in New Mexico, and nearly 100 species at Algodones Dunes in California.) A major reason for the vitality of dune systems is that their soils, being deep and porous, can soak up and store large quantities of water; this water remains available to the plants, which can therefore enjoy unusually long growing seasons. Where plants are productive, animals find many of their key resources. Dune systems can be very rich in bees, wasps, and other insects tied more or less directly to particular plant communities, and also in birds, reptiles, and small mammals. Many species of plants and animals found on dunes also occur elsewhere. Many others are highly specialized for dune habitats and are largely or entirely restricted to them. For example, some dune plants have unusual horizontal growth forms that help them avoid being buried when the sand moves, and many have special adaptations for extracting nutrients from the seemingly sterile soils.

Deserts as a whole contain remarkably large numbers of species in many taxonomic groups. Deserts can have local diversities in some plant and animal groups that are comparable to or even greater than those of the richest temperate and tropical environments. Not all major groups of organisms do well in deserts, of course, especially those that are fundamentally adapted to aquatic environments. Thus deserts tend to be rich in rodents, lizards, and insects, but not in large mammals, frogs, and fishes. But some groups that we think of as "wet" have desert-adapted forms that also reach high diversities—for example, algae, mosses, and lichens.

Two large and important animal taxa that reach their peak diversities in temperate arid regions (including true deserts) are the bees and their close relatives, the sphecid wasps. Local diversities of 400 to 500 species of bees have been recorded at Riverside and Palm Springs, California; these are the highest known bee diversities in the world. On regional scales, too, there are usually more species in the Southwestern U.S. than east of the Mississippi. The entire Eastern U.S. has about 900 species of bees, while Wyoming and California have 700 and 2,000, respectively. Bee populations in the tropics are less well known than those of North America and Europe, but the best estimates indicate that tropical bee diversities are lower than those that occur routinely in intact arid temperate habitats. For example, fewer than 100 species occur in the tropical forests of Barro Colorado Island, Panama (a Smithsonian Institution biological research station), and the total for all of Panama is below 400. Similar patterns occur in other parts of the world. For example, more than 1,000 species of bees are recorded for Spain, but only 240 for Britain. Sphecid wasps are less well studied than bees, but they too appear to reach their highest diversities in arid regions. For example, more than 200 species are known to inhabit a small and fairly homogeneous region of the San Rafael Desert of Utah.

In the Southwest, soils are often recently derived from the weathering of underlying rocks. Some species of plants have become so highly adapted to the structures and mineral compositions of particular soils that they occur *only* where the parent geological formation is exposed. Many of these plants have recently been found to support (and depend on) equally specialized pollinators.

Mountains have climates and soils different from those in the intervening low valleys. They are equivalent to islands in a "sea" of hotter, drier habitat. As on oceanic islands, local adaptation and speciation often occur on neighboring mountaintops, adding further to species diversity. During extended periods of relatively dry climates, some groups that formerly lived in the valleys become stranded on the mountains, often speciating in isolation; then when conditions become wetter, they disperse through the valleys to other mountains, thereby increasing local as well as regional diversity. At present the American Southwest is in a relatively dry phase, and scores of high mountain ranges are home to hundreds of species of plants and animals that occur on only one or a few neighboring ranges.

The surprisingly great biological diversity found *within* deserts is matched by an equally impressive diversity *among* deserts—not only on a global scale, but also among regions in close proximity to each other. For example, the Mojave, Sonoran, Chihuahuan, and Great Basin deserts of the Southwest have very different patterns of rainfall and temperature, with profound consequences for the kinds of biological communities that can evolve and persist in each. The same is true on a finer scale within each of these major deserts. As a consequence, distinctly characteristic suites of plants and animals occur in each desert and in various habitat types within them, and these suites often include species and even assemblages that occur nowhere else.

Unique Attributes of Desert Organisms and Communities

If deserts are so rich biologically, then why isn't this more obvious? The answer lies in the nature of successful adaptations to the climatic factors that create deserts in the first place: temperature and rainfall. Deserts occur where annual precipitation is low and temperatures are high for at least some part of the year. In any form this combination would make water a major limiting factor. Additionally, where rainfall is low on average, it also tends to be relatively *unpredictable*. This unpredictability is believed to be every bit as important as the overall amount of precipitation. Thus *all* desert organisms must have ways to endure or escape relatively unpredictable periods of high temperature and extreme dryness. Conversely, they must also be able to exploit relatively unpredictable periods of moderate temperature and wetness. An important consequence is that, possibly more than in any other environments on earth, life in deserts is *pulsed* and *below-ground*. There's a lot of life in the desert, but to see it you have to be there at the right times, and you have to look in the right places.

Sleep

At their largest characteristic scales, the temporal pulses are seasonal. They can be very dramatic. For example, some perennial plants spend most of the year as a low, inconspicuous, and seemingly dead basal rosette; then they suddenly produce a few leaves, flower, and die back again. Many annuals appear for only a few weeks in the winter or spring, when they may literally blanket the ground, but otherwise spend their lives as seeds in the soil. In years without sufficient rain they may not appear at all. Many animals are similarly opportunistic and intermittent. For example, the famous spadefoot toads may appear in vast numbers in ephemeral pools following a rainstorm.

Seasonal cycles are not unique to deserts, of course. In many temperate habitats small plants die back or overwinter as seeds; trees lose their leaves; insects become inactive for much of the year; and vertebrates tend to hibernate, stay hidden, or migrate. But in deserts the periods of inactivity are much longer, and they occur at opposite times of year from those in more mesic regions. Visiting New England in the "dead" of winter, you would have to spend considerable effort to see much more than dormant trees; this would not surprise you, because you know that winter is only a temporary hiatus. But few people are familiar with the seasonal cycles of deserts, and visits tend to occur in the summer, when the contrast with mesic areas is greatest.

The *daily* rhythms of deserts are also dramatic. Heat stress and the associated problem of water loss are much less severe at night than during the day, so many desert plants and animals do most of their work at night. Most small mammals such as kangaroo rats emerge only after the sun goes down, as do many snakes, owls, insects, spiders, scorpions, and other arthropods. Only then does it become obvious how dense the populations of many species really are.

What can plants do at night? They cannot capture photons, but they can respire. By concentrating their respiration at night when temperatures are lowest, they can greatly reduce the rate at which they lose water to the atmosphere. Some desert plants carry this strategy to amazing lengths: They trap CO_2 only at night when water loss through open stomates is minimized. Then they reduce the stored CO_2 to sugar by day when radiant energy is available to drive the reaction, but they keep their stomates closed to conserve water. These and other remarkable adaptations of desert plants may eventually prove invaluable to agriculture, as water becomes increasingly scarce and expensive in many parts of the world.

Dig

The second major way to escape the heat and to minimize water loss is to live underground. Most desert animals burrow to some extent, and many do so spectacularly. For example, biologists attempting to excavate the nests of desert bees must often continue to depths of four, five, or even six feet. In one case that we know of, a burrow smaller in diameter than a pencil was followed to a depth of eight feet, at which point the investigators gave up in exhaustion, and in fear that the walls of the excavation might collapse on them.

Plants, too, have gone underground in a big way. The tap roots of some shrubs and trees are extremely long, and up to 80 percent of the total plant biomass may be *below* the surface. This compares to 50 percent for plants of mesic temperate regions such as Eastern deciduous woodlands, and perhaps 10 percent or less for tropical moist forests.

Indeed, desert plant communities can be viewed geometrically as inverted rain forests. The latter are famous for their multi-layered canopies, where different species compete fiercely for available light; yet their root systems are very shallow, in part because obtaining enough water is seldom a problem. Desert species, by contrast, have root systems of many different structures and overall depths, through which they compete fiercely for available water; their above-ground branch and leaf systems can be "shallow," however, because light is not limiting. The beautifully regular spacing exhibited by many desert shrubs and bunchgrasses is a direct consequence of their competition for water.

Invent

To cope with the difficulties and opportunities presented by desert environments, plants and animals have evolved many remarkable adaptations. Some examples have already been mentioned, but to emphasize this important aspect of biological diversity in deserts, we will describe a few more of the many thousands of special characteristics found in desert organisms.

The list of ingenious methods for obtaining and conserving water could be extended indefinitely. Some of the more spectacular examples occur in coastal deserts such as the Namib of Africa and the Atacama of South America, where average yearly rainfalls can be less than one inch but fogs occur regularly. Some beetles and other arthropods of the Namib have evolved special behaviors and morphologies that enable them to condense water on their bodies and roll the droplets toward their mouths. In the Atacama, atmospheres near the ground are almost never saturated, so it is not possible to condense water on a chemically neutral surface at ambient temperature (i.e., dew never occurs). Instead, some of the local plants and animals have special salt glands that hygroscopically concentrate water vapor from clear, unsaturated atmospheres.

Another prominent adaptive theme in deserts is *defense*. For example, because water limits the growth rates of individual plants, perennials tend to be slow-growing and long-lived. Individual creosote bushes may often live for hundreds of years, and many relatively inconspicuous species are believed to live for decades. Because a slow-growing plant cannot afford to lose much tissue to herbivores, desert perennials are often tough, spiny, or laden with chemicals that make the plant distasteful to herbivores.

Animals have also invented some clever defenses against both the dryness and each other. Since green plants tend to be either ephemeral or chemically protected, plant material is available to the animal world largely in the form of "baby plants," invisible to the casual human observer. The seeds of annual and perennial plants support many specialized birds, mammals, and insects, which together comprise the most important class of desert consumers. Seed-eating birds must subsidize the high energy cost of flight, so sparrows and finches tend to be seasonal transients that are present only during periods of peak seed production. Resident seed specialists include kangaroo rats (*Dipodomys*) and pocket mice (*Perognathus*), which hibernate or aestivate in comfortable underground quarters both to avoid extreme temperatures and to wait out periods of resource scarcity. There are many species in these highly successful North American genera, which share a number of specialized adaptations found nowhere else. For example, they can obtain all of their water through digestion, and they conserve it by concentrating their nitrogenous wastes into essentially dry excretia.

Also unique to these small mammals are the fur-lined, external cheek pouches that allow them to gather many seeds on the long foraging trips that they must make in order to collect sufficient quantities of their dispersed and ever-changing foods. Their long foraging trips expose them to predators, and this is a principal reason (in addition to temperature) why they are active almost exclusively at night. Although they can avoid hawks in this way, the night is full of owls and snakes for whom small nocturnal seed eaters are a primary resource. Kangaroo rats are virtually bipedal, with strong, enlarged hind limbs and long tails that enable them to accelerate explosively and in unpredictable directions when they detect an attacking owl or snake; their abilities to detect predators are enhanced by disproportionately large eyes and ear cavities.

Another group of seed specialists—desert ground squirrels belonging to the genus *Spermophilus*—is unusual in being active during the day. The undersides of the ground squirrels' large, flattened tails are white, and they carry them curled up over their backs like umbrellas to shield their bodies from the brilliant sun.

Seed-harvesting ants are the other prominent class of resident seed consumers. Large stores in underground granaries sustain their colonies through long droughts. The stores are replenished by intense collecting activity during brief seasonal peaks of seed production. Competition among colonies maintains a nest spacing as regular as that of desert shrubs. For example, the large raised domes of *Pogonomyrmex* nests stand out almost like pieces on a checkerboard when viewed from the air, in many arid grassland regions of Nevada, Arizona, and Utah. The pebble-covered nest mounds are part of an architecture that precisely regulates the nest's interior climate during both summer and winter; this design might well serve as a model in our own search for practical solar heating systems.

A few ant species manage to survive in deserts without relying on seeds. "Honeypot ants" of the genus *Myrmecocystus* gather plant exudates both from floral nectaries and from aphids, which they tend on green vegetation. Aphids suck plant juices, filtering out much of the nitrogen for their own needs, and secreting the remaining sugary liquid as an appeasement gesture to ants. Instead of eating the aphids, worker ants "milk" them like cows, in the process protecting them from predators and parasites. Green vegetation is unavailable for much of the year, however, so hundreds of worker ants serve their nestmates by acting as living barrels in which the nectar can be stored. Hanging from the roofs of nest galleries, the members of this "honeypot" caste keep the nectar fresh and available in their enormously swollen abdomens. The honeypots are relished by coyotes and badgers, which excavate the nest chambers when heavy rains permit digging in the otherwise hard soils. Early Native Americans also satisfied a sweet tooth in this way.

The list of special desert adaptations is almost endless. It includes some that tend to evolve repeatedly in deserts throughout the world, and others (like many of those just mentioned) that seem to have been invented only once and are therefore found only in one group of related species in a single desert system.

In short, deserts are amazingly full of life. They often support large numbers of species, large numbers of individuals, and large numbers of special morphologies, habits, and life histories that adapt desert species to the unique demands and opportunities that arise in variable, arid environments.

Economic, Ecological, Scientific, Educational, and Recreational Values of Deserts

Even though they support little agriculture, deserts are of enormous economic importance. A large fraction of the earth's land surface—a quarter to a third depending on the definition used—is arid or semiarid. If greenhouse warming raises the average temperature even one degree Celsius, as seems very likely, then arid regions could grow to 40 percent of the total land surface or even more. Thus for reasons of scale alone, we need to understand deserts and other arid ecosystems.

In addition to supporting low-density livestock grazing, desert plant communities provide many "ecosystem services" of direct economic benefit. For example, they are vitally important in controlling runoff and erosion. The American Southwest is drained by several major river systems that have been dammed. The plant and animal communities that cover the enormous drainages feeding into these rivers determine the rates at which sediment enters the rivers and is subsequently deposited in the reservoirs behind our dams. Many of these reservoirs are silting up at rates that will render them virtually useless in less than a century. The dams were very expensive to build, and their sites are literally irreplaceable. So there is a staggering cost associated with any major shortening of the expected lifetime of a dam and a correspondingly large benefit associated with the maintenance of intact plant communities throughout their drainages. Damage to these plant communities by overgrazing and poorly regulated off-road vehicle use is a major factor contributing to the high rates at which many reservoirs are now filling up with sediment.

All the members of a plant community contribute in one way or another to the retention of water and the stabilization of soils. One particularly important and unusual component in Southwestern deserts is a complex symbiotic association between lichens and blue-green algae, called cryptogamic crusts. Because they live directly on the surfaces of relatively soft, porous soils, cryptogamic crusts are very effective in reducing erosion, but they are highly vulnerable to disturbance. They also contribute to the establishment of vascular plants because they fix atmospheric nitrogen, which is often a critical limiting nutrient, and they appear to enhance uptake of several other essential elements by plants that have a major portion of their root mass in the cryptogamic crust. Damage to cryptogamic crusts is easy to see and may remain both visible and ecologically significant for decades. Less obvious is the damage to root systems of vascular plants that may also be caused by motorized vehicles. Although many perennial plants send their roots to great depths in the search for relatively permanent groundwater, many others specialize in the rapid collection of rainwater and therefore develop delicate, highly ramified root systems that are concentrated just below the ground surface. These plants can be seriously harmed even if their above-ground parts are untouched.

Like rain forests, deserts contain a largely unknown and untapped wealth of plant and animal species that could provide useful products of many kinds, either directly or through future transfers of their genes into domesticated species. The well-developed chemical defenses of many plants provide one of the more obvious lines of exploration. For example, the evergreen, perennial bearclaw poppies of the Mojave-Great Basin transition zone are a cornucopia of alkaloids. The three species share at least 16 alkaloids distributed among four distinctly different structural classes. These compounds seem to provide an effective deterrent to herbivores, since the large, soft leaves of these poppies are rarely eaten by invertebrate or vertebrate herbivores; the one exception is a tiny mealybug that appears to be specialized for eating these plants.

Many kinds of desert organisms are likely to contain valuable genetic resources, because of their special adaptations to extreme conditions. For example, another common evergreen plant of the American Southwest, creosote bush, often provides most of the green foliage available in its habitat for months on end. One would think that such a source of succulent forage would be avidly harvested by a wide variety of starving herbivores, but the foliage of creosote bush is rarely eaten. The leaves are coated with a layer of phenolic resins of bewildering structural diversity. The resins may account for as much as 44 percent of the weight of expanding leaves and 15 percent of mature leaves. The resins are obviously distasteful, and when eaten they appear to reduce the digestibility of the tissue by binding proteins in such a way that the resin-protein complex cannot be absorbed from the animal's digestive tract. As a consequence, consumers get little nutritional reward and turn to other, less abundant species of plants.

Deserts have been and will continue to be very important scientifically. The physiologies of desert plants and animals are of fundamental interest for the same reasons they are of potential economic interest—because they are adapted to relatively extreme conditions. Deserts have also been very important in scientists' elucidation of the processes that shape and organize natural communities. Patterns indicative of these processes can be obscure in a fully three-dimensional forest, but they often stand out starkly in the relatively two-dimensional (above-ground) world of the desert. It was in deserts that the importance of root competition was first appreciated. Regular differences in the body sizes of co-occurring granivores (both rodents and ants) provided some of the earliest and most convincing evidence that body-size differences can reduce competition between animal species and thereby facilitate their coexistence.

For terrestrial communities, the first experimental evidence of competition between taxonomically unrelated consumer species came from deserts. Certain rodents and ants compete for seeds, and removal of either group leads to immediate population increases of the other. But remarkably, the rodents actually benefit the ants in the long run. The seeds eaten by rodents are, on average, slightly larger than those taken by ants, and give rise to larger seedlings that are stronger competitors than those of smaller-seeded species. If rodents are removed, the larger-seeded plant species gradually increase in density, suppressing the smaller-seeded plants on which ants rely. As a consequence, some species of ants virtually disappear where rodents have been suppressed for periods of a decade or more. Complex ecological interactions of this kind are likely to be important everywhere, but it is much more feasible to study them in deserts than almost anywhere else.

Aside from their intrinsic advantages for many kinds of biological research, deserts are uniquely important because they contain some of the earth's largest remaining tracts of relatively undisturbed land, where biological communities survive more or less in their natural states (i.e., with relatively few extinctions and introductions of exotic species). In the future there may be few other places on earth in which such communities will be able to survive. Thus deserts will have very great importance as "natural laboratories" both for research and for education.

The importance of deserts to geology and paleontology is widely understood, but most people are surprised to learn that they are of special importance to climatology as well, and that the reason is biological. Pack rats of the genus *Neotoma* continuously occupy rocky nest—sites in which they collect many kinds of plant material. Because nest sites may be inhabited for hundreds or even thousands of years, and because they occur in dry places above the soil, the accumulated litter provides a continuous record of the plant communities that occurred at that site over a long period. Samples of this ancient plant material can be carbon-dated, allowing records from widely separated localities to be correlated with each other. Thus through painstaking excavations of packrat middens and analyses of their contents, investigators are building up a detailed picture of the effects of climate change during the last 10,000 years or more. This knowledge is of great scientific interest. It may prove to be of great practical importance as well in helping us to predict the effects of future (human-induced) climate change.

Deserts have enormous aesthetic and recreational value. They are places of sublime beauty where people of average means can safely experience true wilderness, stunning geology, and profound solitude. Many people currently place a high value on these experiences, and many more are likely to do so in the future as our population becomes both more urbanized and better educated.

The stereotype of deserts as voids would seem to imply that they could not even in principle be damaged, because a "nothing" cannot be harmed. But as we have shown, deserts are far from empty, and they are *more* vulnerable to serious disruption than are many other kinds of environments. This vulnerability is a direct consequence of their aridity. We mentioned that a low average availability of water is coupled with a high variance in its availability. Plants therefore tend to live "closer to the edge" in deserts than elsewhere, so that relatively small changes in external conditions can cause relatively large effects on the plant community, with corresponding effects on the animals. In short, deserts can all too easily be "desertified"—stripped of much of their plant and animal life.

Biologically diverse and productive communities have often been impoverished through overexploitation, especially in arid parts of the world such as the Mediterranean and Persian Gulf regions. This process has always been tragic, in the fullest sense of the word, for the peoples of those regions—and all the more so because the difference between sustainable and unsustainable patterns of exploitation may have been fairly small. But the damage was effectively irreversible, and many kinds of values (economic, ecological, scientific, educational, aesthetic, and recreational) were severely compromised for all time.

We do not mean to suggest that the only way to preserve the life of deserts is to keep people out of them. Indeed, the best way to create a constituency for our North American deserts is presumably to show people, first-hand, what rich and interesting places they really are. But owing to their fragility, deserts are unlikely to survive the increased levels of disturbance that will occur unless we learn to manage them in an informed and far-sighted way that takes account of their unique characteristics and the full range of their present and future values.