

Small Mammals in Hot Deserts: Some Generalizations Revisited

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Life originated in aquatic environments and secondarily invaded terrestrial habitats. This invasion entailed coping with radically different physical environments that vary most noticeably from aquatic ones in that they are desiccating, highly variable in temperature, and often suffused with intense shortwave radiation. This contrast reaches its extreme in deserts, the most terrestrial of environments. Deserts can be defined as regions in which precipitation is so low, so infrequent, and so variable that it plays the dominant role in controlling biological productivity (Noy-Meir 1973). Most deserts combine this lack of water with seasonal periods of high temperatures. This combination of heat and aridity produces a profound challenge for animals, including mammals.

Mammals, regardless of the habitats they occupy, typically maintain core body temperatures of approximately 37–38 °C. As a result, their primary thermoregulatory problem in most nondesert regions is to maintain body temperature above environmental temperature. For example, mammals may cope with the low temperatures characteristic of cold winters or polar regions by an exaggeration of the primitive mammalian characteristic of a high capacity for metabolic heat generation combined with substantial insulation. In hot deserts, however, high air temperatures, combined with intense solar radiation, produce conditions in which environmental temperature substantially exceeds body temperature. Effective thermoregulation must therefore rely on a mechanism that will move heat out of the body against a temperature gradient. The only such mechanism known in organisms is evaporation of water, which is driven not by temperature gradients but by differences between the water vapor pressure at the animal's surface and in the surrounding atmosphere. To thermoregulate, therefore, desert mammals must use the single resource whose paucity defines these habitats. This requirement provides the fundamental difficulty for mammals occupying hot deserts.

The combination of heat and aridity reaches its extremes in the global belts of subtropical deserts that are located near latitudes 30° N and 30° S. These deserts include the Sonoran Desert, the Sahara Desert, and the Australian deserts. Summers in these regions can be extraordinarily hot. The typical human experience during a summer day in the core of a hot subtropical desert is a combination of ovenlike air temperatures, intense radia-

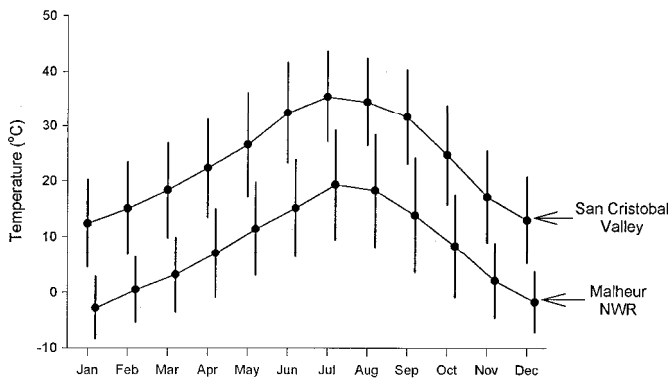
DESERT RODENTS MAY EXPERIENCE HIGHER TEMPERATURES AND GREATER ARIDITY THAN HAS GENERALLY BEEN APPRECIATED; MUCH REMAINS TO BE LEARNED ABOUT THE PHYSIOLOGICAL MECHANISMS THAT ALLOW THESE ANIMALS TO TOLERATE EXTREME HEAT AND TO MAINTAIN HYDRATION

tion from the sun as well as the hot soil surface, and the absence of surface water. Under such conditions, unprepared people may survive for only a few hours.

Despite such apparent hostility, subtropical deserts are also famous for the diversity of life found within them. The Sonoran Desert, for example, lies in the southwestern United States and northwestern Mexico and is inhabited by 61 species of mammals (Hall 1981). (This number excludes bats, whose exceptional mobility makes them a special case.) The majority of these mammals are rodents, a diverse group whose members play important roles in desert communities as modifiers of soil structure, consumers of plants, and prey for other animals. This success is striking because their small size prevents them from traveling to the few and widely spaced sources of surface water. The challenge for desert rodents, therefore, is to occupy these extraordinarily hot environments without drinking.

Not surprisingly, the ability of animals to function in desert environments has received much attention from biologists. Indeed, animal physiological ecology began its rise to prominence with the publication of seminal contributions about desert animals by workers such as George A. Bartholomew, Raymond A. Cowles, William R. Dawson,

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Bodil Schmidt-Nielsen, and Knut Schmidt-Nielsen. Despite the extensive focus placed on desert organisms, however, many of the most common generalizations accepted in textbooks and taught to generations of students become questionable under careful scrutiny, in part because of insufficient appreciation for the wide variety of conditions presented by deserts, and in part because of the tendency to study animals exposed to more moderate conditions than those more typical of hot subtropical deserts. In this article, I discuss current knowledge—and its weaknesses—about the thermal and hydric environments experienced by small desert mammals and the physiological mechanisms that allow them to occupy these environments.

The climate experienced by small desert mammals

Perhaps the most familiar generalization about desert climates is that heat stress is ameliorated by low atmospheric humidity; “it’s a dry heat” (e.g., Schmidt-Nielsen 1964, Cloudsley-Thompson 1965, Louw and Seely 1982). In addition, two well-known conclusions have followed from the observation that, as is typical for small mammals in all environments, desert species usually occupy burrows and are active on the surface only at night. In the Sonoran Desert, for example, 93% of rodent species are nocturnal.

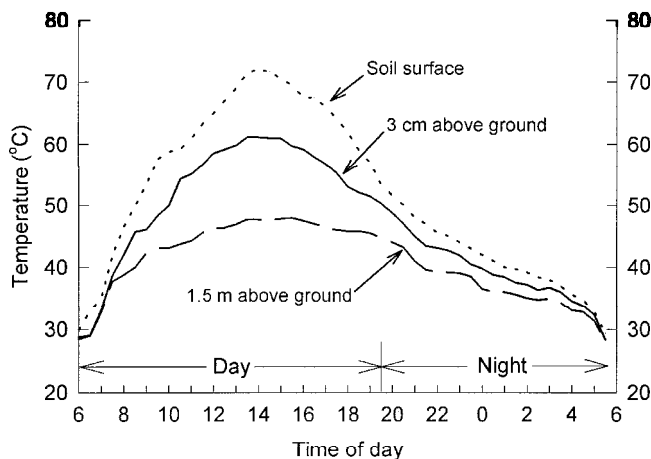


Figure 1. The annual cycle of air temperature in two desert sites. Values represent the daily range between the average minimum temperature and the average maximum temperature. The San Cristobal Valley (represented by data from Dateland Ranch in Yuma County; Sellers and Hill 1974) lies in the Sonoran Desert of southwestern Arizona. Malheur National Wildlife Refuge is in the Great Basin Desert of eastern Oregon. Data are from NOAA (1985).

(The exceptions are four species of ground squirrel.) Because environmental temperatures decline dramatically after sunset, this finding led to the generalization that restricting activity to the night allows animals to evade the very high temperatures that are characteristic of daylight hours (e.g., Schmidt-Nielsen 1964, 1990, Louw and Seely 1982). An associated conclusion was that subterranean burrows provide cool, humid retreats for desert animals during daylight hours (e.g., Schmidt-Nielsen 1964, 1990, Louw and Seely 1982). Consequently, small mammals are usually portrayed as alternating between a cool, humid burrow during the day and the warm, dry atmosphere of the desert soil surface at night.

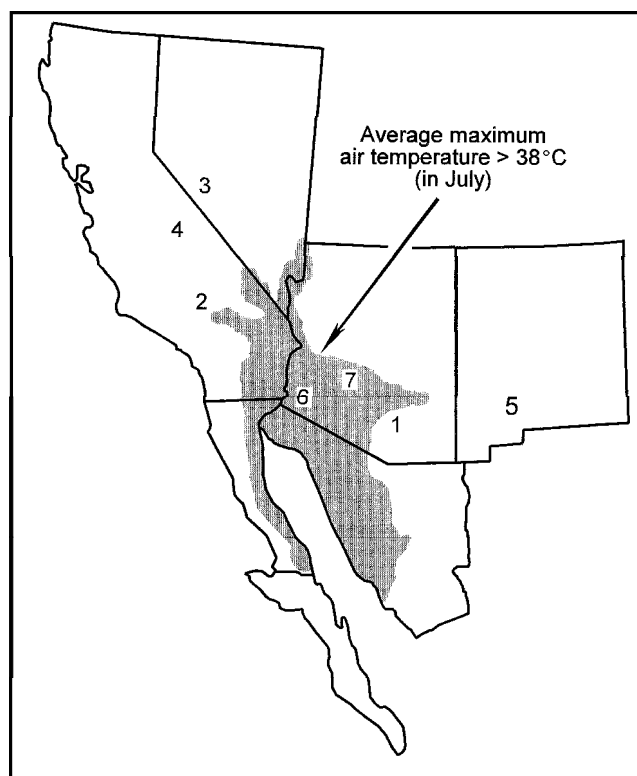
Environmental temperatures experienced by small desert mammals.

The climates that are actually experienced by desert rodents can differ sharply from these traditional generalizations and may be much more challenging. For example, although nocturnal temperatures do typically decline 15–20 °C below diurnal maxima in many desert regions (Sellers and Hill 1974, Pearce 1990), the consequences of this drop differ greatly among desert regions. Within hot subtropical deserts, average daily maxima during summer months are commonly so high (42–46 °C) that such drops only reduce nocturnal minima to 26–30 °C (Sellers and Hill 1974, Pearce 1990)—much warmer than the nocturnal minima of deserts located at higher altitudes or latitudes.

In both a subtropical Sonoran Desert site (the San Cristobal Valley in Arizona) and one in the northern Great Basin Desert of the western United States (Malheur National Wildlife Refuge in Oregon), for example, air temperature typically varies approximately 16–17 °C over the

Figure 2. Average surface and air temperatures in July in the central Sonoran Desert. Data are averages for 10–27 July 1996 for sand dunes in the San Cristobal Valley, Yuma County, Arizona. Data for 1.5 m and 3 cm above the soil surface were collected using thermocouples shielded from solar radiation and thermal radiation from the soil surface. Surface temperature was measured within a 1 m² area using six thermocouples connected in parallel with each other to average local variations. Surface thermocouples were coated with a thin layer of local dust so that they possessed radiative properties similar to the soil with which they were in contact.

Figure 3. The hottest desert regions in the United States. Within the shaded area, maximum daily air temperature in July exceeds, on average, 38 °C. Data are from Sellers and Hill (1974) and NOAA (1985). Numbers identify locations of field studies of the subterranean environment of desert rodents: 1, Vorhies (1945), Schmidt-Nielsen et al. (1948), Schmidt-Nielsen and Schmidt-Nielsen (1952); 2, Lee (1963); 3, Hayward (1965); 4, Kenagy (1973); 5, Kay and Whitford (1978); 6, this article (Figure 2); 7, this article (Figure 4).



daily cycle (Figure 1). Temperatures in the Great Basin Desert site, however, average 16 °C below those in the Sonoran Desert site (Figure 1). As a result, afternoon maximum temperatures on a typical summer day in the northern site are similar to the lowest temperatures experienced at night in the subtropical desert. Indeed, July temperatures in the northern site are similar to those of March or November in the southern desert. Clearly, the conditions experienced by mammals differ substantially between the deserts. Therefore, the consequences of traits such as nocturnality also differ. In the subtropical desert habitat of the San Cristobal Valley, for example, nocturnality allows animals to avoid very high afternoon temperatures that peak in July, on average, at 48 °C at a height of 1.5 m above the ground (Figure 2). Nocturnality does not simply equate, however, to avoidance of high temperatures. Nighttime temperatures during July average 36.4 °C, and the air temperature typically drops below 30 °C for only 1 hour per night.

Moreover, all of these temperatures represent unrealistically cool indexes of the thermal environments experienced by typical desert animals because they reflect measurements made within meteorological enclosures placed approximately 1.5 m above the ground. Most mammals weigh less than 50 g and live only a few centimeters above the ground, where the air is usually much hotter due to solar heating of the soil surface (Cloudsley-Thompson 1965, 1991, Louw and Seely 1982, Nobel 1983). The effects of solar heating occur not only during daylight hours but also at night, when heat stored in desert soils substantially elevates air temperatures (Figure 2). During July in the San Cristobal Valley, for example, the average nocturnal temperature experienced 3 cm above the ground is 38.8 °C—more than 2 °C higher than the temperature 1.5 m above the ground.

Finally, it is important to recognize that data such as those in Figure 2 represent mean values around which considerable variation occurs. Of course, organisms do not merely have to cope with average conditions; they must also survive the extremes. The hotter portions of the Sonoran and Mojave Deserts normally experience several 7–10 day episodes each summer in which air temperatures remain substantially above average. Even at heights of approximately 1.5 m, air temperatures in such extreme periods reach 45–50 °C during the day and drop to only 28–32 °C at night. Therefore, even solely nocturnal ani-

mals may routinely experience high temperatures while above ground.

In addition to facing high temperatures on the soil surface at night, desert rodents also experience much warmer temperatures within their subterranean retreats than is generally appreciated. Data quantifying burrow temperatures at locations occupied by desert rodents are sparse, but measurements supporting the view that burrows provide cool retreats were supplied by Vorhies (1945), Schmidt-Nielsen and Schmidt-Nielsen (1950, 1951, 1952), Lee (1963), Hayward (1965), Kenagy (1973), and Kay and Whitford (1978). These studies, however, were conducted outside the hottest deserts (Figure 3). In these more moderate regions, rodents such as kangaroo rats (*Heteromyidae: Dipodomys* spp.) place their nest chambers at depths of 30–60 cm below ground (Vorhies 1945, Schmidt-Nielsen and Schmidt-Nielsen 1950). Burrow depths in the hottest desert regions apparently are similar. We have excavated six burrows of Merriam's kangaroo rat (*Dipodomys merriami*) in the San Cristobal Valley, in the core of the Sonoran Desert, and have found that nest chambers, which are the deepest portion of the burrow, are 40–60 cm below the surface (Randall L. Tracy and Glenn E. Walsberg, unpublished data). At these depths, soil temperatures are high (e.g., 38–41 °C; Figures 4 and 5). Even if other species dig more deeply, burrows more than 2.5 m deep would be required to reach soil temperatures below 30 °C during summer months in the central Sonoran Desert. Given that burrowing is energetically demanding and time consuming (e.g., Vleck 1979), the necessity to dig very deep burrows could substantially alter

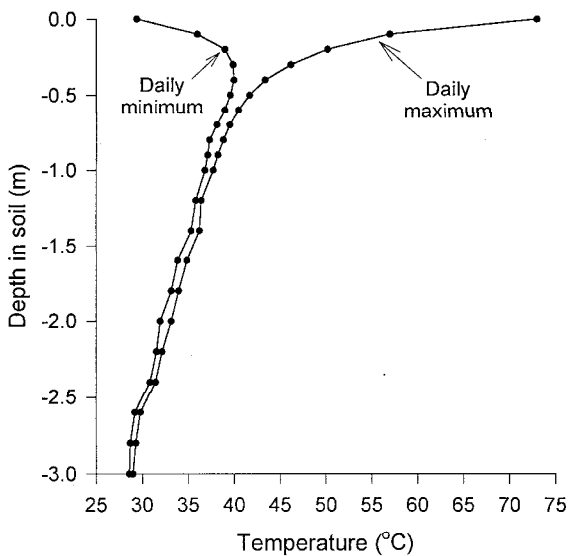
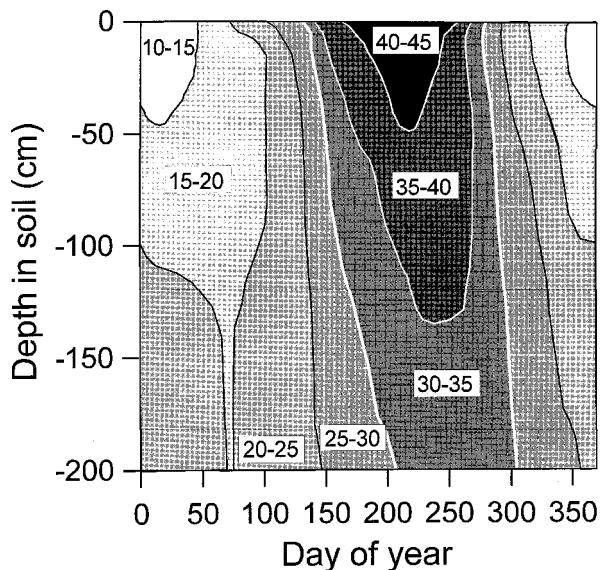


Figure 4. Daily maximum and minimum soil temperatures during summer in the Sonoran Desert. Data are average values collected during 10–27 July 1996 in the San Cristobal Valley, Yuma County, Arizona, using 1 mm diameter thermocouples placed at 10 cm intervals at depths of 0–1 m, and at 20 cm intervals at depths of 2–3 m.

the animal's time and energy budget as well as constrain its thermoregulatory options.

Humidities experienced by small desert mammals.

The portrayal of desert animals as experiencing high humidity while in their burrows and low humidity above ground may not be correct. The expectation of low humidity above ground can be deceptive for two reasons. First, humidities are often reported as relative humidity, which is the fraction of water vapor contained in ambient air compared to the maximum that the air could hold at its prevailing temperature. This index therefore subsumes both air temperature and water content. However, saturation vapor density is an exponential function of air temperature, and high temperatures in themselves produce lowered values. For example, 26% relative humidity at 45 °C represents the same absolute humidity (in terms of g/m^3 of H_2O in air) as 100% relative humidity at 20 °C.



Absolute humidity is a better index for evaluating effects on organisms because it, not relative humidity, sets the gradient for evaporative cooling.

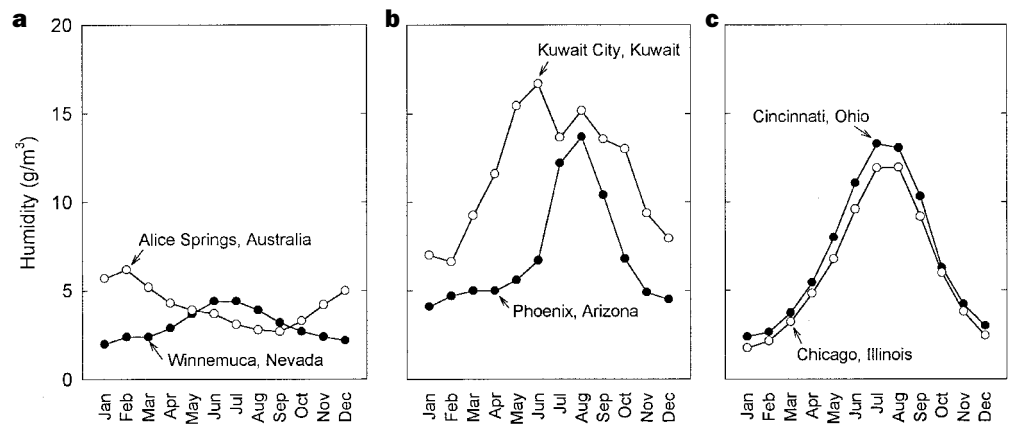
The generalization that atmospheric humidities are low in desert regions is deceptive for an additional reason: many subtropical deserts receive seasonal influxes of humid tropical air. Such influxes are a notable feature of the Chihuahuan Desert, the Sonoran Desert, and portions of the Sahara, Arabian, and Middle Eastern Deserts (Figure 6). In these regions, absolute humidity levels can be quite high (e.g., $10\text{--}15 \text{ g/m}^3$), similar to those of deciduous forest regions notorious for humid summers (Figure 6).

Another common view is that burrows occupied by desert mammals provide humid environments that significantly reduce evaporative water loss. However, this generalization is based on studies by Vorhies (1945) and Schmidt-Nielsen and Schmidt-Nielsen (1950, 1952) in the Santa Rita Experimental Range in southern Arizona, an area that is not truly arid. Annual rainfall in this area averages 50 cm, far more than the 8–25 cm that is typical of the Sonoran Desert (Sellers and Hill 1974). In addition, the Schmidt-Nielsen's data were collected during a period (May–June 1948) in which soils were probably unusually moist; 10 cm of rain fell in the 2 months preceding their field work (Sellers and Hill 1974). Indeed, basic soil physics dictates that the 100% relative humidities reported for cavities in the ground can be produced only if the surrounding soil is saturated with water (Jury et al. 1991), a highly atypical condition for deserts. Similarly, Vorhies (1945) measured humidity within kangaroo rat burrows during a 21-month period in 1930 and 1931, two extraordinarily wet years in which total precipitation was 71 cm and 97 cm, respectively (Sellers and Hill 1974).

Several factors are likely to oppose high humidity levels within burrows. The most obvious is that desert soils are normally dry. The humidity within a soil-confined air space can be calculated from measurements of soil water

Figure 5. Annual cycle of average daily soil temperature in a Sonoran Desert site. Daily minima and maxima vary greatly from average values in the upper levels of the soil (e.g., Figure 4). Data were collected by Kenneth M. Wooden from creosote bush scrub 30 km north of Gila Bend, Maricopa County, Arizona. Data were collected at 0, 10, 20, 30, 40, 60, 80, 100, 125, 150, and 200 cm below the soil surface using thermocouples as described for Figure 4. Values were collected over 24 hours at 4-week intervals throughout 1998 and then interpolated to form best-fit isotherms.

Figure 6. Average humidity values for six different desert and temperate sites. (a) Desert regions with persistent low humidity. (b) Desert regions that receive a seasonal influx of humid air masses. (c) Temperate regions with high humidity. Data were computed from those in Sellers and Hill (1974) for Phoenix, Arizona; from those in NOAA (1985) for Winnemucca, Nevada; Cincinnati, Ohio; and Chicago, Illinois; and from Pearce (1990) for Alice Springs, Australia, and Kuwait City, Kuwait.



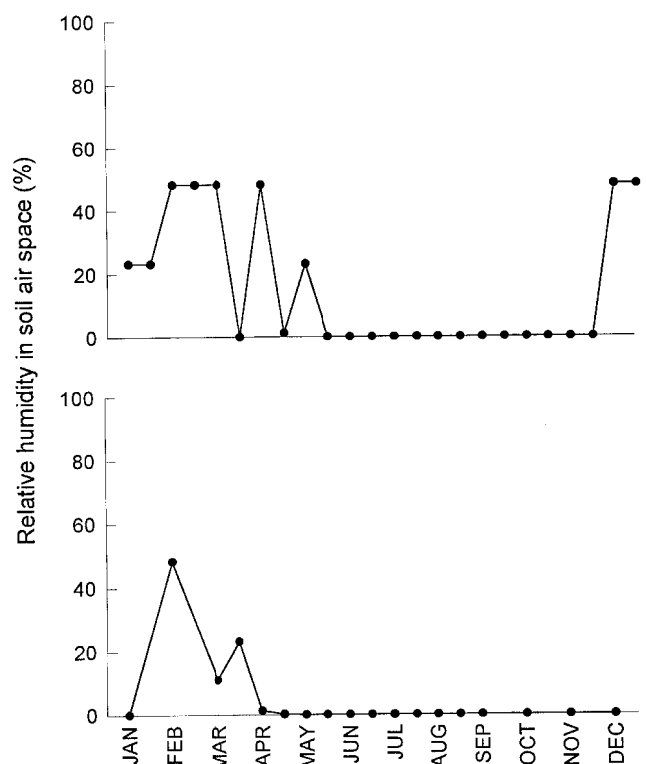
potential. Examples of such data for the Sonoran Desert include those of Szarek and Woodhouse (1977) and Monson and Smith (1982). Except for periods immediately following rainfall, humidity in soil air spaces is calculated to be extremely low (Figure 7). In addition, desert soils are normally dominated by mixtures of gravel, sand, and clay. The relative porosity of sandy soils (Jury et al. 1991) allows vapor to diffuse from an occupied burrow, and the strongly hygroscopic nature of clay particles also tends to reduce humidity in soil-confined air spaces (Jury et al. 1991). Finally, desert animals generally minimize evaporative water loss, which in turn minimizes animal-induced elevations of burrow humidity. For example, evaporative water loss for kangaroo rats typically totals only approximately 70 mg/hour (MacMillen and Hinds 1983).

Predicting the overall consequences of these factors on burrow humidity is challenging because they depend on the geometry and ventilation of the burrow system, the rate at which the animal supplies water vapor to the air space, and a suite of soil properties affecting vapor diffusion. Although empirical measurements of the humidity of occupied burrows have yet to be completed, I offer two types of crude estimates. One is derived by calculating vapor efflux from a nest chamber using Campbell's (1977) equation for diffusion from a spherical surface and making five assumptions: the nest is in a 16 cm spherical cavity (Vorhies 1945, Kenagy 1973) with a plugged entrance (if the entrance were open, vapor would be lost and humidity reduced); the animal releases water vapor at 70 mg/hour (MacMillen and Hinds 1983); vapor leaves the chamber

Figure 7. Humidity within soil air spaces in the Sonoran Desert. Values were calculated from the equation for the relation between soil water potential and relative humidity in Campbell (1977), using data describing soil water potential at either 30 cm (top; Szarek and Woodhouse 1977) or 40 cm (bottom; Monson and Smith 1982) below the soil surface.

only by diffusion through the soil air space (i.e., air is not convected out of the chamber, nor do soil particles adsorb water molecules, both of which would decrease humidity); the diffusivity of water vapor through the soil air space is 30 mm²/s, a reasonable value for dry, sandy soils (Jury et al. 1991); and the burrow is deep in the soil (more than 1 m; being closer to the soil surface would facilitate vapor loss and decrease humidity). Such calculations indicate that, even within a completely sealed nest chamber, humidity would rise to no more than 4 g/m³ over a 10-hour period (Figure 8).

A second method of estimation is to supply water vapor to a nest-sized cavity within desert soil and to measure the resulting humidity. In June, I constructed six 16 cm wide cavities, 1 m deep and at least 30 m apart, in silty desert soil 45 km east of Gila Bend, Maricopa County, Arizona.



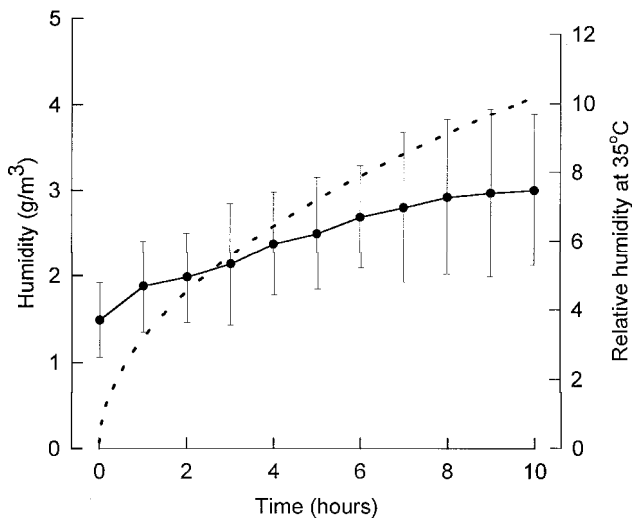


Figure 8. Estimated humidity within a burrow. The dashed line shows an estimate based on calculated rates of water vapor diffusion through the soil; the solid line shows an estimate based on empirical measurements of humidity in soil cavities supplied with water vapor at rates approximating that released by a kangaroo rat. See text for details. Vertical bars represent 95% confidence intervals. The time scale indicates hours after the animal's entry into a sealed nest chamber.

The cavities had a metal ceiling to prevent collapse, and measurements were made in mid-June, 3 months after excavation, to allow the soil to settle. Water was added to the chamber at a rate expected for evaporative loss from a kangaroo rat by injecting liquid water at a rate of 0.07 ml/hr through 1 mm diameter polyethylene tubing extending to the chamber interior. The water dripped onto filter paper placed on the chamber floor and evaporated. Humidity within the chamber was measured using the methods of Walsberg and Wolf (1995). Similar to the results of the calculations above, these experiments suggest that water vapor accumulates slowly in an occupied burrow (Figure 8). Even within a chamber sealed for 10 hours, vapor densities averaged only 3 g/m³ (i.e., 7% relative humidity at 35 °C). It thus appears improbable that burrows in dry desert soils reach high humidities, although resolution of this issue will clearly require empirical measurement of humidity within occupied burrows.

In summary, although desert mammals are often portrayed as alternating between a cool, humid burrow during daylight hours and a warm, dry atmosphere on the desert soil surface at night, the reality may be very different, and much more challenging, for species occupying subtropical deserts. Rather than being cool, burrows may be quite hot. Temperatures below 30 °C may be available only if the animal is able to excavate to great depths. Humidities within burrows are probably low most of the time. On summer nights, both soil and air temperatures commonly remain high. Finally, heat stress on surface-active animals may be exacerbated by seasons of high humidity in some desert regions.

Generalizations about physiological responses

Given the truly harsh conditions faced by small desert mammals, their survival is remarkable. Critical features of an animal's physiology that affect its ability to occupy such climates include the range of environmental temperatures

that is tolerated, how narrowly the animal's body temperature is regulated, the degree to which such tactics as torpor are used to avoid seasonal shortages of water or energy, and the animal's major avenues of water gain and loss. Although solutions evolved by small mammals are diverse, a series of important generalizations about the physiology of desert mammals have been developed.

Environmental temperature tolerance. Desert mammals are usually divided into two functional groups: those that tolerate prolonged exposure to high temperatures, and those that have limited tolerance to such conditions. The small mammals that are most clearly tolerant of high environmental temperatures are those that are active almost entirely during daylight hours. Indeed, diurnal forms, such as the antelope squirrels (*Ammospermophilus harrisi* and *Ammospermophilus leucurus*) and the round-tailed ground squirrel (*Spermophilus tereticaudus*), are typically active on the soil surface for prolonged periods during very hot summer days (Vorhies 1945, Dengler 1967, Chappell and Bartholomew 1981, Kenneth M. Wooden and Glenn E. Walsberg, unpublished data).

In contrast to such high-temperature tolerance, many nocturnal desert rodents, such as kangaroo rats, will apparently survive only limited exposure to high environmental temperatures. Body temperature in kangaroo rats resting quietly at ambient temperatures below 35 °C is typically 37–38 °C (Carpenter 1966). At ambient temperatures above 35 °C, body temperature increases. Environmental temperatures of 38–40 °C are rarely tolerated for more than 1 hour before the animal dies (Carpenter 1966). Tolerance is further reduced when animals exercise at intensities typical of surface activity. In Ord's kangaroo rats (*Dipodomys ordii*) exercising by running for periods of less than 20 minutes, body temperature is regulated at approximately 1.5–3.0 °C above resting levels (Wunder 1974). Even at mild environmental temperatures of 25–30 °C, however, *Dipodomys* apparently cannot limit this increase if they continue to exercise, and their body temperatures will rise to lethal levels (Wunder 1974).

Such limited tolerance to high temperatures suggests that rodents occupying truly hot desert areas cannot remain active for prolonged periods when exposed to normally prevailing conditions. In the central Sonoran Desert, for example, there may be less than 3 hours per night during which air temperatures 3 cm above the

ground fall below 35 °C, a kangaroo rat's apparent limit for sustained exercise, and there are less than 5 hours per night during which temperatures fall below the lethal limit of approximately 38 °C for a kangaroo rat resting quietly (Figure 2).

Heterothermy in normally active animals. The role of temporal heterothermy in the physiology of small mammals is unclear. By contrast, for large desert mammals, diurnal cycles of hyperthermia have been demonstrated in several species, including dromedary camels (*Camelus dromedarius*), Grant's gazelle (*Gazella granti*), and oryx (*Oryx gazella*; Schmidt-Nielsen et al. 1957, Taylor 1970). When these animals are exposed to high temperatures, their body temperature rises approximately 5–7 °C over the course of a day. By tolerating such variation, their dependence on evaporative cooling, which would otherwise be needed to maintain lower body temperatures, is reduced. The large size of these animals and consequent low surface-area-to-mass ratio means that the time course of heating and cooling is relatively long, occurring over major fractions of a 24-hour period. As a result, body temperature can drop passively at night and rise slowly during the course of a day.

Some small rodents exhibit similar substantial elevations in body temperature when exposed to high ambient temperatures. A salient example is the antelope squirrel (*A. leucurus*), which inhabits hot deserts in North America. Free-living antelope squirrels exhibit short-term (less than 1 hour), major (4–5 °C) variations in body temperature when active during hot summer days (Chappell and Bartholomew 1981). Unfortunately, neither the basis for this variation nor its role in reducing evaporative water loss is clearly understood. Bartholomew (1964) described a behavioral cycle in which the animal is intensely active on the hot soil surface, allowing its body temperature to passively rise to 42–43 °C, and then retreats to a cool burrow and rapidly lowers its body temperature without resort to evaporation by such behaviors as pressing its abdomen to the cool burrow floor. Although this description is frequently reproduced in textbooks and reviews, it was a speculation based on the range in body temperature observed in squirrels held in the laboratory. The pattern Bartholomew (1964) presented was not derived from data for free-living animals (Hudson 1960, Bartholomew and Hudson 1961), nor has subterranean behavior such as pressing the abdomen to the burrow floor been shown to be responsible for the variations in body temperature measured by Chappell and Bartholomew (1981).

The most extreme heterothermy known in desert rodents occurs in the round-tailed ground squirrel, which inhabits low-lying, hot basins in the Mojave and Sonoran Deserts. Over a range of air temperatures from 10 °C to 45 °C, body temperature varies from 30 °C to 42 °C while the animal maintains apparently normal levels of activity and responsiveness (Kenneth M. Wooden and Glenn E. Wals-

berg, unpublished data). Such extreme heterothermy has important implications for the understanding of both the biology of desert animals and the evolution of the mammalian pattern of thermoregulation. For desert forms experiencing environmental temperatures that exceed body temperature, increasing body temperatures will reduce the thermal gradient driving heat into the animal, consequently decreasing reliance on evaporative cooling and aiding in conserving water. Depression of body temperature at low environmental temperatures also would reduce energy expenditure.

Perhaps more important, the use of broad heterothermy raises questions about the selection pressures underlying the evolution of mammalian and avian patterns of thermoregulation. Both taxa maintain relatively constant and high body temperatures. Constancy of body temperature is usually viewed as advantageous because organisms comprise complex suites of biochemical reactions, all of which typically exhibit strong temperature dependence (e.g., Hochachka and Somero 1984). Homeothermy therefore allows biochemical systems to evolve to function best at a single temperature, which is clearly important for coordination of the system as a whole.

Why do birds and mammals maintain relatively high body temperatures? The answers to this question are complex and the subject of debate, but a common theme is that reaction rates increase at high temperatures, thus facilitating the animal's ability to respond quickly and powerfully to stimuli (e.g., Bennett and Ruben 1979, Hochachka and Somero 1984, Pough et al. 1996). Broadly heterothermic mammals that apparently maintain normal capacities for activity therefore present an important puzzle. If animals such as the round-tailed ground squirrel can maintain normal levels of activity and responsiveness over temperature ranges of more than 10 °C, then why do other mammals not do the same? What mechanisms have broadly heterothermic mammals evolved that allow them to achieve this flexibility, and what are the associated physiological costs and benefits? It may well be that understanding the functioning of these species could yield insight into the critical mechanisms and selection pressures involved in the evolution of high-temperature homeothermy in general.

Hypothermy in inactive animals. Facultative and profound reductions in core body temperature occur in many groups of small mammals, including those of desert regions (e.g., Heteromyidae, Sciuridae). During episodes of such hypothermia (torpor), physiological functions are substantially depressed. Most notably, metabolic power consumption typically drops 90–95%. In addition to such reductions in resting power consumption, the great reduction in the animal's activity also contributes to overall reductions in energy demands. Torpor therefore represents an important tactic for reducing energy demands during periods when little food is available. Persistent use

of torpor during winter is commonly referred to as hibernation; that during late summer and early autumn is labeled estivation. During periods of such seasonal dormancy, animals are not continuously torpid; rather, they arouse at intervals that are temperature dependent. For example, at low environmental temperatures (e.g., less than 5 °C), pocket mice may be continuously torpid for many days at a time, whereas at higher temperatures they may arouse daily (French 1993). Animals are not usually active on the surface during such arousals. In northern desert regions, therefore, pocket mice may spend 9–10 months continuously underground (French 1993).

Studies of hibernation have focused mainly on torpor at low environmental temperatures, often near freezing. In subtropical deserts, of course, the much warmer soils have potentially major effects on both the seasonal extent of hibernation and the energy savings achieved. Although it is unclear how low soil temperatures must be for an animal to enter torpor, average soil temperatures below 20 °C may be available for only a few months a year, and average temperatures below 10 °C may simply not exist in subtropical deserts (Figure 5). In addition to the shorter periods of time in which torpor can be used, animals in subtropical deserts may not be able to reduce body temperature as much as species occupying cooler deserts. Metabolic power consumption in torpid animals is an exponential function of body temperature, which, above critical limits, tends to parallel environmental temperature. In *Perognathus longimembris*, for example, a 10 °C increase in body temperature elicits an approximately 2.5-fold increase in metabolic rate (i.e., $Q_{10} = 2.5$; French 1993). As a result, even if body temperature were reduced to that of the lowest subsurface temperatures in the central Sonoran Desert (15–20 °C), metabolic power consumption would be approximately 2–4 times higher than at the much lower temperatures characteristic of hibernators in cold climates. Warm soils may thus greatly diminish the energetic benefits of hibernation.

The mammals that enter dormancy at perhaps the highest environmental temperature are those that estivate, including the Mojave ground squirrel (*Spermophilus mohavensis*) and the round-tailed ground squirrel. Mojave ground squirrels reside in the Mojave Desert of California and enter dormancy in late August (Bartholomew 1964). Round-tailed ground squirrels occupy the hotter Sonoran Desert and enter estivation in late September. Except for a few individuals that may be seen on the surface throughout this period, these squirrels remain below ground without access to food or water until early February (Kenneth M. Wooden and Glenn E. Walsberg, unpublished data). Soils are very warm when round-tailed ground squirrels enter estivation (typically around day 270 in Figure 5), averaging approximately 33–35 °C to at least 2 m below the soil surface. During early estivation, therefore, body temperature cannot be below 33–35 °C, which does not suggest great energy savings. The advantages of such high-

temperature dormancy, and the animal's physiological status during this period, therefore remain unclear.

Water balance. A pervasive generalization regarding small desert mammals is that many species survive on a diet of dry seeds without drinking. Although this generalization is broadly accepted (e.g., Schmidt-Nielsen 1964, 1990, Louw and Seely 1982, Pough et al. 1996), its validity is open to question. The most famous and extensively studied desert animals that are considered to survive on a dry diet without drinking are heteromyid rodents, particularly kangaroo rats. Indeed, analyses of the physiology of kangaroo rats provided a prototypical case history in physiological ecology (Schmidt-Nielsen et al. 1948, Schmidt-Nielsen and Schmidt-Nielsen 1950). The survival of kangaroo rats under such conditions is largely attributed to their ability to conserve water by producing highly concentrated urine (e.g., 5020 mOsm/kg in *Dipodomys merriami*; Christopher 1975) and relatively dry feces (46% H₂O; Schmidt-Nielsen and Schmidt-Nielsen 1951) and to minimize evaporative water losses.

Nevertheless, evaporation appears to be the major path of water loss in *Dipodomys*, with most water lost from the respiratory tract. This pulmonary evaporation is significantly reduced by the nasal counterflow system (Jackson and Schmidt-Nielsen 1964). Inhaled air flows over a large area of moist membranes covering the nasal turbinate bones. This influx of dry air evaporates water from the nasal mucosa, consequently chilling it. During exhalation, warm, moist air exhaled from the lungs again passes over this chilled mucosa, cooling the exhaled air and condensing moisture onto the nasal mucosa, thus conserving both heat and water within the animal (Schmidt-Nielsen et al. 1970). Although this nasal counterflow system reduces respiratory water loss by more than two-thirds and therefore is particularly beneficial to desert species, the adaptation is not unique to them. Extensive nasal turbinates—the thin, scroll-shaped bones that provide the surface area for condensation of water vapor—occur in most mammals regardless of habitat, and the counterflow mechanism is apparently a general feature evolved early in mammalian evolutionary history to reduce the dehydration otherwise produced by maintenance of high body temperatures (Hillenius 1992). As a consequence, for example, the effectiveness of the nasal counterflow system in rodents that occupy more mesic habitats, such as common laboratory rats (*Rattus norvegicus*), is similar to that of xeric-adapted kangaroo rats (Jackson and Schmidt-Nielsen 1964).

The fact that nasal reclamation of exhaled water is a general feature of mammals, regardless of habitat, refocuses attention on other mechanisms acting to reduce pulmonary evaporation in arid-adapted rodents, such as the comparatively low rate of metabolic power consumption of heteromyid rodents (French 1993). Oxygen consumption in these species is approximately 25% lower, on aver-

age, than in other mammals. Assuming that their oxygen extraction efficiency is equivalent to that of other mammals, the lower oxygen consumption should decrease the amount of dry air passed through the respiratory tract, consequently reducing evaporative water loss. Overall, evaporative water loss in kangaroo rats is less than in most other mammals, averaging approximately $1.7 \text{ mg}\cdot\text{hr}^{-1}\cdot\text{g}^{-1}$ at low temperatures. Evaporation is minimal, however, only at low to moderate temperatures. At ambient temperatures above 35°C , water loss increases rapidly (MacMillen and Hinds 1983).

The ability of such rodents to persist in deserts has traditionally been attributed to the combination of these impressive abilities to conserve water with the microclimatic amelioration associated with being nocturnal and fossorial (e.g., Schmidt-Nielsen and Schmidt-Nielsen 1951). It is striking, therefore, that analyses of *Dipodomys* have demonstrated water balance only at temperatures that are relatively low for a subtropical desert. Schmidt-Nielsen and Schmidt-Nielsen (1951) calculated that water balance could be maintained in moderate humidities if air temperatures remained below 25°C . Based on their field work, they concluded that burrow temperatures or surface temperatures at night rarely exceed 25°C and that a humid atmosphere within burrows significantly reduces water loss. As I have already noted, however, such conditions are probably atypical during summer in subtropical deserts. In fact, aboveground temperatures may drop below 25°C only occasionally, and burrow temperatures may never drop below 25°C .

More recent analyses suggest that the maximum temperature at which rodents achieve water balance may often be much lower than this. MacMillen and Hinds (1983) analyzed data for five genera and 13 species of heteromyid rodents and found that the temperature at which metabolic water production (the major source of water if the animal consumes dry seeds) balances evaporation (the major avenue of water loss) in a dry atmosphere varies significantly with body mass. The smallest forms (pocket mice; *Perognathus* and *Chaetodipus*) achieve water balance at the highest temperatures, but the maximum temperature known for maintenance of water balance for any species is only 26°C . Temperatures rarely get this low during summer in the hotter subtropical deserts. The temperature calculated for metabolic water production to balance evaporative loss on a dry seed diet in kangaroo rats is even lower, at $16\text{--}17^\circ\text{C}$ (MacMillen and Hinds 1983). Such temperatures are certainly unavailable for months at a time in hotter regions. Thus, physiological data would seem to indicate that these species cannot survive on a dry diet when exposed to the climates that they normally occupy.

To identify answers to this puzzle, it may be necessary to examine routes of water balance long considered to be unimportant. One answer may be that the assumption that species such as kangaroo rats consume only dry seeds is incorrect. Although the possibility that these animals

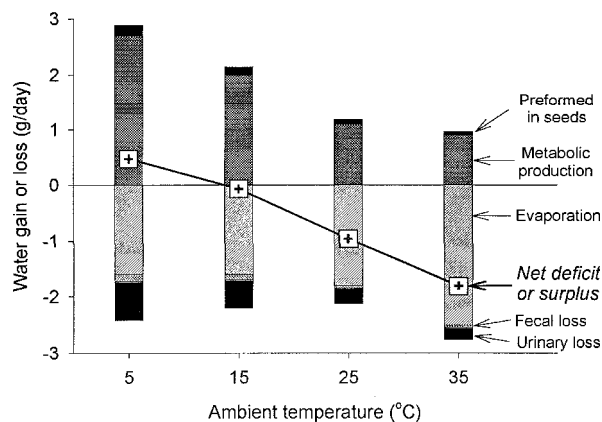


Figure 9. Projected water balance for a 35 g Merriam's kangaroo rat on a diet of dry seeds at different ambient temperatures. Graph shows sources of water gain (metabolic production and preformed in seeds) and loss (evaporation and loss in feces and urine). Plus symbols in squares indicate net water balances. Metabolic water production and evaporative water loss were calculated from the mass-specific values of MacMillen and Hinds (1983). Values for the minor components of the water budget were calculated based on estimates of food consumed and associated amounts of feces and urine produced. The mass of seeds consumed was calculated using Schmidt-Nielsen's (1964) ratio of seed mass to metabolic water production ($53.7 \text{ g of H}_2\text{O per 100 g of seed}$). Preformed water in the seeds was estimated as 3.7% of seed mass (Schmidt-Nielsen 1964). Fecal water loss and urinary water loss were assumed to be proportional to mass of food ingested and to equal 2.5% and 13.5% of intake, respectively (Schmidt-Nielsen 1964).

obtain significant amounts of water from succulent food was discarded early in analyses of their biology (Vorhies 1945, Schmidt-Nielsen and Schmidt-Nielsen 1951, Schmidt-Nielsen 1964), it merits reexamination in light of the finding that kangaroo rats consume substantial amounts of green vegetation and insects (Reichman and Price 1993). For example, Reichman (1975) found that, averaged over a 2-year period, the diet of Merriam's kangaroo rat consisted of 78% seeds, 16% insects, and 6% green vegetation. Assuming that seeds contain 10% water, insects 70% water, and green vegetation 90% water, the ingested food averaged 24% water.

This crude approximation demonstrates that, by consuming small amounts of succulent food, desert rodents can more than double the preformed water acquired compared to that obtained by consuming seeds exclusively. This largely unappreciated potential for water intake is supported by data for water turnover in free-living animals. From Mullen's (1971) data for *D. merriami* collected using isotopically labeled water to estimate body water turnover and carbon dioxide production in the field, Nagy and Peterson (1988) calculated that the ratio of water to

energy in the diet is 1.3–3.0 times that expected if this species consumed only dry seeds. Nagy and Peterson (1988) consequently suggested that “these animals are obtaining more water in the field (probably by ingesting more succulent food) than expected from laboratory studies.” This analysis strongly hints that preformed water may comprise an important component of the water budget of *Dipodomys* in nature.

The potentially critical role of such an auxiliary water source can be illustrated by some simple calculations. During summer in the central Sonoran Desert, rodents may experience average environmental temperatures of around 35 °C, even if their burrows are approximately 1.5 m deep and they restrict their activity to cooler periods of the night (Figures 2 and 4). At this temperature, kangaroo rats on a dry seed diet will dehydrate. To avoid dehydration, a 35 g Merriam’s kangaroo rat would have to acquire roughly 1.8 g/day of water (Figure 9). Aside from toxic shrubs such as creosote bush (*Larrea tridentata*), green vegetation can be essentially absent from much of the Sonoran Desert for major portions of the summer. Cacti, the most famous succulent plants, are often sparse in the plains of the central Sonoran Desert. However, insects, which average approximately 70% water by mass, are available, and kangaroo rats are known to eat them (Reichman 1975, Reichman and Price 1993). If a kangaroo rat consumed insects to meet its water deficit, then a 35 g rodent would have to locate and consume approximately 2.6 g of insects (i.e., more than 7% of its body mass) per day. Such insectivory presents a considerably different image of the ecology of this common rodent than that of being solely granivorous and independent of preformed water.

In contrast to the heteromyid rodents, some other small mammals are well known to depend on succulent food, such as cacti and other green vegetation, as a source of water. Although consumption of succulent vegetation mitigates the most obvious problem of dehydration for the animal, it by no means provides a perfect solution to problems of water balance. Animals’ quest for water may present severe threats to water-storing plants, which, not surprisingly, have evolved mechanisms to defend against herbivores seeking water. Defenses include both obvious physical devices (e.g., thorns), as well as less conspicuous chemical defenses. For example, creosote bush is a perennial shrub and the dominant plant in the Sonoran, Mojave, and Chihuahuan Deserts. It maintains its leaves through the seasonal droughts, long after most other plants are thoroughly desiccated. Creosote bush is also heavily defended; 10–30% of leaf dry mass is a complex mix of phenolic resins (Mabry et al. 1977, Kenneth M. Wooden and Glenn E. Walsberg, unpublished data). These resins repel potential herbivores by their taste, combine with proteins in the animal’s digestive tract to render them indigestible, and are directly toxic (Mabrey et al. 1977, Karasov 1989). Nevertheless, some small mammals feed

extensively on creosote bush. During the late-summer drought in portions of the Sonoran Desert, for example, creosote bush constitutes almost the entire diet of round-tailed ground squirrels (Kenneth M. Wooden and Glenn E. Walsberg, unpublished data).

The consequences for both individuals and populations of dependence on a toxic plant for a water source may well be profound, but they have received little attention. The best-studied species that relies on creosote bush as a water source during the summer and autumn in the Mojave Desert is the desert wood rat (*Neotoma lepida*; Karasov 1989). Although the plant’s water content is adequate to satisfy the animal’s water demand, wood rats are apparently limited in their consumption of *Larrea* by the plant’s resin content and consequent toxicosis. It is ironic, therefore, that during the summer and autumn drought, wood rats have ready access to the creosote bush’s green leaves yet lose body mass and may become emaciated. The smallest animals apparently die (Karasov 1989). Thus, survival evidently depends on an individual’s capacity to tolerate toxins as well as on the water and resin content of the local creosote bushes.

Concluding comments

Desert mammals occupy habitats that present extraordinary demands, and they meet these challenges with evident success. Despite the long history of studies of these animals, however, it is remarkable that fundamental aspects of their biology remain obscure. Initial results from research in my laboratory, for example, indicate that researchers have underestimated critical features, such as the ability of some desert rodents to tolerate high environmental temperatures or to conserve water through mechanisms such as production of highly concentrated urine. In part, this underestimation reflects a lack of appreciation for the degree to which the physiological responses of small mammals can vary, even within a small geographic range. Within a single subspecies of kangaroo rat (*D. merriami*), for example, critical factors such as evaporative water loss vary substantially between portions of the Sonoran Desert that are separated by distances of only approximately 200 km but contrast in heat and aridity. However, it remains the case that physiologists cannot account for the abilities of desert mammals to persist in harsh deserts on a dry diet.

This lack of understanding is particularly unfortunate because comprehending the ecological physiology of desert mammals may provide insights, not only into the biology of these species but also into the physiological bases for the occupation of terrestrial habitats in general. The importance of developing such an understanding is amplified by the prospect of significant increases in global temperatures during the next century. Although the degree and distribution of global warming is still unclear, current estimates indicate unprecedented rates of climate change. Within the present subtropical deserts, these

changes may create hyperthermal deserts characterized by environmental temperatures exceeding those of any large-scale habitat now existing.

Although it is not yet possible to make even coarse predictions of the consequences such warming will have for desert animals, several effects are possible. One is that higher temperatures could critically reduce the time available for surface activity. In the core of the Sonoran Desert, for example, nocturnal rodents presently may have only approximately 5 hours during a summer night for surface activity at air temperatures below 38 °C. A 3 °C increase in average air temperature would reduce this period by approximately one-half (Figure 2). In addition, soils in subtropical deserts are already heated deeply (e.g., 30 °C at 2.5 m below the surface; Figure 4). During mid- to late summer, the average annual soil temperature represents the lowest temperature existing in the soil. Although this average annual temperature does not vary substantially with depth, during the hottest months it will occur only at depths below 5–7 m, at which both daily and seasonal cycles are effectively damped (Jury et al. 1991). Data reported in Figure 5 indicate that average annual soil temperature in the central Sonoran Desert is currently approximately 27 °C. Given that no desert mammal is known to burrow 5–7 m below the surface, a 3 °C temperature increase would mean that only subterranean temperatures above 30 °C would be available.

In addition to imposing additional heat stress, warmer soils could also substantially reduce the energy savings associated with seasonal dormancy. A 3 °C elevation of burrow temperature and, consequently, of the body temperature of a torpid rodent would increase metabolic power consumption approximately 32% (if $Q_{10} = 2.5$). Compounding this effect, shorter periods of the annual cycle may be available for hibernation. If a small rodent requires burrow temperature to be below 20 °C to initiate dormancy, for example, then a 3 °C elevation in annual cycles of soil temperature in the central Sonoran Desert would reduce the length of time that torpor can be used by roughly 25% (Figure 5).

Given these possibly large-scale effects, the extent to which small mammals will be able to persist within increasingly hotter subtropical deserts becomes open to question. Clearly, it is time to examine more critically the biology of these organisms, which play key roles in desert communities.

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