

Water, Salts, and Excretion

at Work: Mammals of Deserts and Dry Savannas

In deserts, large herbivores such as the oryxes in this photograph are usually the equivalent of nomads, moving about to find moisture to survive. Similarly, in the dry savannas—the grassland plains—large herbivores often function as nomads or migrants. Conditions vary so much from time to time and from place to place in these arid zones that living in an invariant locale is often not a viable strategy. The same can be said for humans in a state of nature; most of the traditional cultures of the deserts and dry savannas were nomadic.

Our goal in this chapter is to explore how the oryxes and other species of sizable mammals—5 kg or larger in body weight—can live in hot deserts or dry-savanna ecosystems. One way to understand these mammals is to compare them with small species, so we will sometimes mention the kangaroo rats, gerbils, and other small mammals that coexist in arid habitats with the large species. However, the small mammals were discussed in Chapter 28, and we will not return to them here in any detail. The mammals of Africa will receive greatest emphasis because they form the most diverse and abundant set of large, arid-land mammals in the world today, and their diversity has drawn the interest of physiologists for decades.

Desert and Dry-Savanna Environments

Deserts and semideserts by most accountings cover about a third of the land on Earth. There is no uncomplicated way to define a desert. One of the simplest definitions is that a desert receives less than about 25 cm (10 inches) of precipitation per year, but this is an imperfect standard because there are regions that receive much more than that but are undoubtedly deserts. Following the lead of Imanuel Noy-Meir, most biologists prefer a definition that emphasizes two attributes of deserts that are of extreme importance for plants and animals. First, a **desert** is a place where precipitation is so low that *availability of water exerts a dominant controlling effect on biological processes*. Second, *when precipitation occurs in deserts, it comes in infrequent, largely unpredictable events*. Rains in deserts are highly irregular and unreliable in both time and space. One year may bring 5 times (or even 20 times) the rain of another. One 30-km² area may be drenched during a storm while a nearby area of similar size receives nothing, because rains in deserts are usually produced by isolated storms rather than broad fronts. Large herbivores must often conduct their lives in ways that—more than anything—are opportunistic, taking advantage of rain or moisture whenever and wherever it occurs.

The classic look of the **dry savannas** is of endless plains of grass with trees dotted here and there. Taking a big-picture view of Earth,

Oryxes are extreme examples of large mammals that can survive indefinitely in hot deserts without drinking water Physiologists are still learning how these animals orchestrate their water losses and gains to stay in water balance in such water-poor and thermally stressful places. The animals shown are gemsbok oryxes (*Oryx gazella*), often called simply gemsbok.



dry savannas are in many cases neighboring environments to deserts. Gradients of moisture often occur on continental scales of space, with moist forests in some regions, deserts in others, and dry savannas between the two—in intermediate regions where there is more moisture than in the deserts, but far less than in the forests. In dry savannas—as in deserts—water is a dominant controlling factor for biological processes. This is true in a somewhat different way than in deserts, however. Savannas usually have discrete rainy seasons interrupted by discrete rainless seasons. Because of the rainless season each year, although on an annual basis savannas receive more rain than deserts do and receive it more predictably, the plants and animals living in savannas must often endure profound drought for long lengths of time. The Serengeti plains of East Africa are examples of this second sort of water-controlled ecosystem. Routinely during the long dry season each year, no rain falls for 4–6 months; thus streams dry up, and soils become so parched that the grasses turn crisp and brown.

Deserts and dry savannas exist for several reasons. The single most important cause of desert and semidesert conditions on a planetary scale is the global pattern of air movements, whereby air warmed at the equator rises to high altitudes and displaces air at those altitudes in such a way that high-altitude air descends to Earth's surface somewhere else. Air at high altitudes, partly because it is cold (see Table 27.2), contains little moisture, even when saturated with water vapor. Thus, in regions where high-altitude air tends consistently to fall to low altitude, the land can become parched. The present global pattern is for high-altitude air to descend in two bands encircling the globe at latitudes roughly 30° north and 30° south of the equator. Most of the world's great deserts (see Figure 27.6)—including the largest, the Sahara—are products of this process. Another common but more localized cause of desert or savanna conditions is rain-shadowing caused by highlands. If a region's only reliable source of moisture is winds blowing in from the ocean, and if intervening highlands force the winds to rise—so that the air cools and its moisture condenses to form rain or snow—the winds may have little moisture left by the time they blow into the region of interest. Near Los Angeles, for example, the coastal mountains force the prevailing winds blowing east from the Pacific Ocean to rise, causing mountain rain. Seen from above, the land still farther east, the Mojave Desert, looks much like a dry, sandy-colored shadow cast by the mountains.

The existence and extent of deserts and dry savannas, we see, often depend on nothing more permanent than the gossamer movements of air. Accordingly, over the long reaches of geological time, deserts and savannas have come and gone as patterns of air movement have changed. The modern Sahara Desert, for example, has existed for less than 6000 years. Nonetheless, desert conditions have come and gone in North Africa for at least 7 million years. Currently the Sahara Desert is tending to expand north and south. Thus, for example, a recent consensus report by climate scientists concluded that the southern reaches of Europe (e.g., Italy and southern Spain) are likely to become far drier over the upcoming decades.

Despite the variability just discussed, deserts and savannas have probably always existed somewhere. Thus they have long presented plants and animals with special challenges, and they have long presented opportunities for species that are able to make do with little water and tap the meager water resources available.

The Relations of Animals to Water

Large mammals have both disadvantages and advantages compared with small mammals in hot deserts and dry savannas. Many of the most apparent disadvantages of large size are behavioral. Large mammals cannot take shelter underground by digging burrows, as small rodents do, and they are less likely than small species to find adequate shade or other protective microhabitats on the surface of the ground. In hot environments, large mammals therefore confront the heat more directly than small mammals do, and the heat stress they experience can place demands on their water resources. In contrast to the *behavioral* limitations they face, however, large mammals are often in a distinctly more favorable *physiological* position than small mammals are.

Large body size is a physiological advantage in terms of water costs

To explore the physiological implications of body size, let's compare mammals of large and small size while making two simplifying assumptions.¹ Let's assume that the animals *thermoregulate physiologically* by use of evaporative cooling and that they are actually confronted with stressfully hot conditions. For an animal to thermoregulate under such circumstances, it must evaporate water to void from its body not only the *exogenous* heat that enters its body from the hot environment but also the *endogenous* heat produced by its own metabolism. Large body size is an advantage from both of these perspectives.

Speaking of exogenous heat inputs, large mammals enjoy an advantage because they have less body-surface area per unit of weight than small mammals do (their surface-to-volume ratios are lower; see Equation 7.6). When the air temperature is higher than body temperature and the sun is beating down, environmental heat enters an animal's body across its body surfaces. Because large mammals have relatively little body-surface area per unit of weight, they tend to experience less heat entry per unit of weight over a period of time than small mammals do. Thus their water costs to void the incoming heat are lower per unit of weight.

Speaking of endogenous heat inputs, large mammals are in a more favorable position than small ones because of the allometric relation between metabolic rate and body size. Large mammals tend to have far lower weight-specific metabolic rates than small mammals (see Figure 7.9). Thus their rates of endogenous heat production per unit of body weight are relatively low, and their weight-specific water costs to void endogenously produced heat are also low.

Quantitatively, the physiological advantages of large size are dramatic. In the 1930s, D. B. Dill (1891–1986)—a pioneer in the study of exercise and heat—undertook famous “walks in the desert” that provided the very first quantitative information on the water costs of mammalian exercise under hot conditions. He himself was one of the human subjects, and he took along with him both dogs and burros. Together, man and beast trekked under the searing sun in the Nevada desert, sweating or panting to thermoregulate; and as they walked, Dill measured their rates of dehydration. Knut Schmidt-Nielsen (1915–2007), another pioneer in desert research, used fundamental principles and Dill's data to construct the classic line shown in red in [Figure 30.1](#). Later, Dill and collaborators gathered more data of a similar sort on burros and high-school students in

¹These assumptions are not realistic in all cases but bring out important principles.

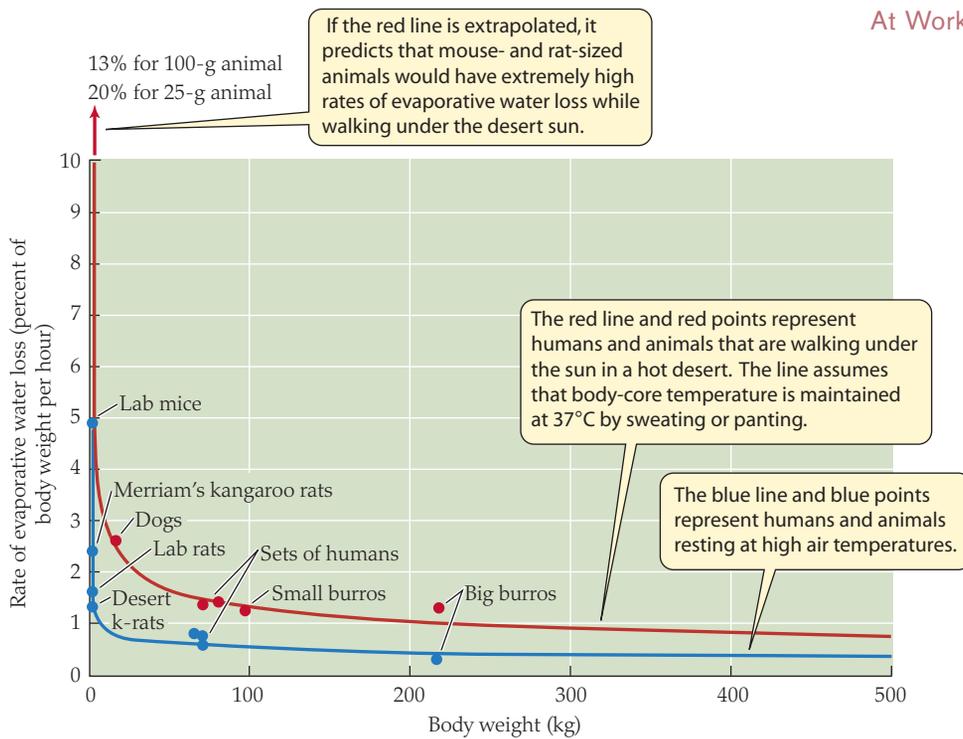


FIGURE 30.1 The rate of evaporative water loss experienced by mammals exposed to heat stress depends strongly on their body size

The graph shows weight-specific rates of evaporative water loss for exercising animals (red) and resting animals (blue) directly exposed to hot conditions. The resting humans and burros were studied while resting in the desert; the resting mice and rats were studied in a laboratory chamber maintained at an air temperature of 40°C (104°F). The equation for the red line is $E = 6.03W^{-0.33}$, where E is rate of evaporative water loss in percentage of body weight per hour and W is body weight in kilograms. The equation for the blue line is $E = 1.38W^{-0.21}$. The two species of kangaroo rats included in the resting studies are Merriam's kangaroo rats (*Dipodomys merriami*) and desert kangaroo rats (abbreviated "desert k-rats"; *D. deserti*), weighing 34 g and 114 g, respectively. (After Schmidt-Nielsen 1954; Sohlt et al. 1977.)

the Colorado desert, accounting (along with Dill's original data) for the five data points plotted in red on the figure.

The red line shows that there is a very strong relation between body size and the water cost of thermoregulation when mammals are active in the daytime desert. The line applies specifically to mammals that thermoregulate at a body temperature of about 37°C as they exercise.² To interpret the line, it is important to recognize that the rate of evaporation is plotted in *weight-specific* terms on the y axis. Specifically, the rate of evaporation is expressed as grams of water lost from the body per 100 grams of body weight during an hour; that is, *percentage of body weight lost per hour*. As you can see, the water cost of being active in the daytime desert is predicted to *soar* at small body sizes.

According to the red line, if a 100-g rat were to walk along under the desert sun and thermoregulate by evaporation of water, its water cost would be almost 13% of its body weight *per hour*. If a 25-g mouse were to do so, its water cost would be about 20% per hour. Dehydration ordinarily becomes lethal under hot conditions when 10–15% of body weight has been lost. Thus the rat walking along under the sun would die of dehydration after about an hour, and the mouse would die after a half hour! In other words, from what we know, it would be *impossible* for rat- and mouse-size mammals to lead fully exposed, active lives in the daytime desert. Of course, rats and mice have never been actually tested to see if these predictions hold true for animals walking under the desert sun. However, the blue line in Figure 30.1 shows actual data for four species of rats and mice—as well as burros and humans—that were studied while resting under milder heat-stress conditions. These data verify that water costs rise steeply at body sizes as small as those of rats and mice. From this perspective, it is indeed fortunate that small mammals can readily escape the full intensity of the daytime desert heat by burrowing and other *behavioral* means.

Physiologically, small mammals are ill-equipped to face the full brunt of desert conditions.

Facing the full brunt of desert conditions, however, is exactly what large desert mammals must often do. And fortunately, as Figure 30.1 shows, large mammals are in a far better physiological position to do so than small mammals. Based on the red line, a 100-kg mammal, such as a small adult burro, can thermoregulate while exercising in the heat of the desert day at a water cost of just 1.3% of its body weight per hour, and a 400-kg mammal, such as an adult dromedary camel, can do so at a water cost of only 0.8% per hour. The water costs of large mammals in the desert are still lower when the animals are not exercising, as shown by the blue line. Large size, in brief, is a great advantage physiologically when animals directly confront hot conditions. This is not to say that all large mammals can solve the problems they face in deserts by the simple evaporation of water; for animals that live where water is almost impossible to find, even a loss as low as 0.8% per hour during midday hours would become life-threatening within a few days. We will see later in this chapter that animals such as oryxes and camels have evolved specific adaptations that enable them to reduce water costs to levels far below the ordinary costs associated with their body sizes.

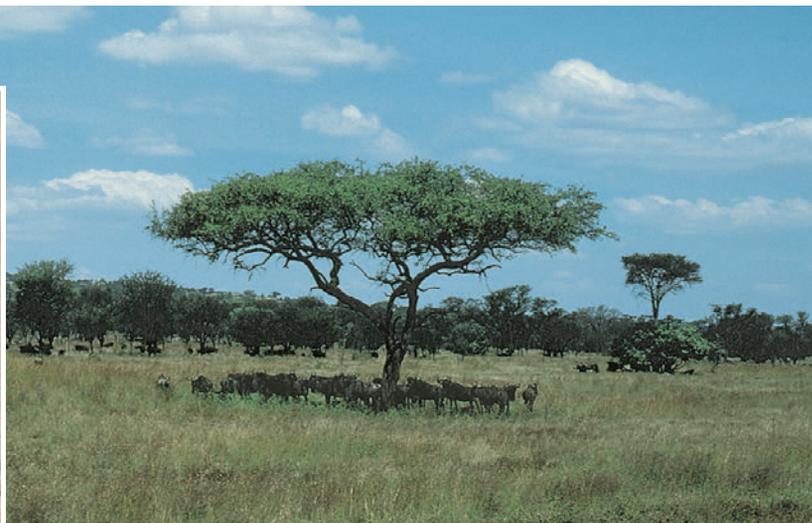
Coexisting species are diverse in their relations to drinking water

One might imagine that all large species of mammals that have long histories in arid environments would have evolved minimal water requirements. That is not the case, however. Among the species that are common in dry, hot places, some are classified as **drinking-water-independent** because they are able to remain healthy for many days or weeks without access to drinking water. Although most of these animals must drink on occasion, some species may be literally independent of drinking water and *never* need to drink. However, other coexisting species are classified as **drinking-water-dependent** because they must drink each day, or at least every other day.

²The humans, dogs, and burros used to construct the line in fact thermoregulate in approximately this way, although not all species do.



FIGURE 30.2 Common wildebeests are drinking-water-dependent antelopes that seek shade. Also called blue wildebeests, common wildebeests (*Connochaetes taurinus*) weigh about 200 kg as adults. They seek shade when it is available, as under the acacia tree in the photograph on the right.



Whether a particular species falls into the drinking-water-independent or the drinking-water-dependent category depends in part on the severity of conditions. A species that is independent of drinking water in the cool seasons of the year might, for example, become dependent in the hot seasons. Despite such ambiguities, the distinction between drinking-water-independent and drinking-water-dependent species is a useful organizing principle for discussing large desert and dry-savanna herbivores.

An outstanding example of coexisting drinking-water-independent and drinking-water-dependent species is provided by the fabled herds of herbivores in the Serengeti ecosystem and other similar ecosystems in East Africa and South Africa. Two of the most prominent drinking-water-dependent species in the Serengeti are wildebeests and zebras.³ During the hot seasons of the year, they must drink every day or every other day. This means, in effect, that

³The species discussed in this paragraph are the common or blue wildebeest (*Connochaetes taurinus*), the plains or Burchell's zebra (*Equus burchelli*), the common eland (*Tragelaphus oryx*; also called *Taurotragus oryx*), Grant's gazelle (*Gazella granti*), and Kirk's dik-dik (*Madoqua kirkii*).

they cannot wander more than about 25 km (15 miles) from standing water. Species that often coexist with wildebeests and zebras, but are drinking-water-independent, include Grant's gazelle, the common eland, and the dik-dik (dwarf antelope). These animals are able to travel far from standing water (because they need not return to it every day), and in that way they gain access to food resources that are unavailable to the drinking-water-dependent species. On even just modestly hot days in areas where trees are found, wildebeests seek shade in the heat of the day (Figure 30.2), whereas Grant's gazelles on such days are indifferent to sun or shade (Figure 30.3). This contrast in shade-seeking behavior correlates with the water physiology of the two species: The species that dehydrates more readily in the absence of drinking water also exploits shade more readily when shade is available.

The most dramatic manifestation of the difference between drinking-water-independent and drinking-water-dependent species in the Serengeti ecosystem is the differential participation of the two categories of animals in the annual migration. The annual migration in the Serengeti is itself perhaps the most dramatic

FIGURE 30.3 Grant's gazelles are drinking-water-independent antelopes noted for their indifference to sun or shade. These gazelles (*Gazella granti*) weigh about 50 kg as adults. Grant's gazelles are one of the species often reputed by naturalists to be able to live indefinitely without drinking water in the dry savannas and deserts.



KEY

- Wildebeests and zebras
- Nonmigratory drinking-water-independent species of herbivores

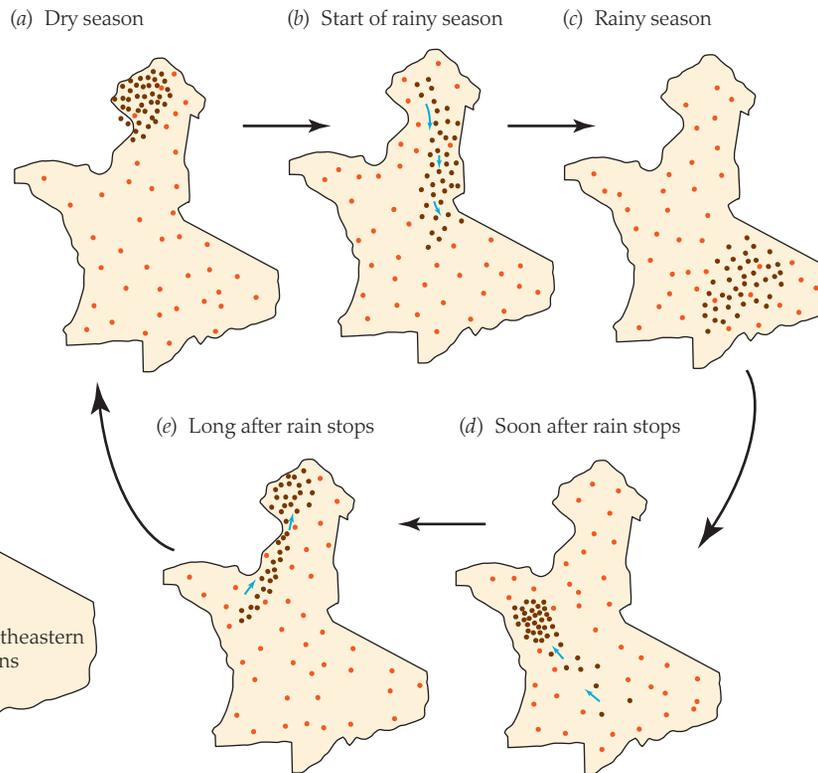
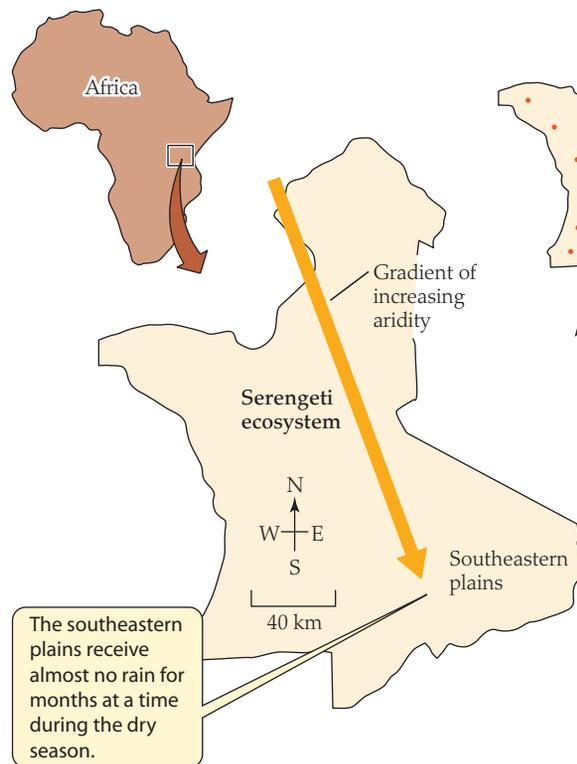


FIGURE 30.4 The annual migration in the Serengeti ecosystem. Driven by seasonal changes of water availability, the drinking-water-dependent wildebeests and zebras migrate from the northwest in the dry season (a) to the southeast in the rainy season (b,c) and back again (d,e), whereas most drinking-water-independent species adjust only in much more subtle ways to the seasonal rhythm of dry and rainy seasons. The Serengeti ecosystem as mapped here includes not just Serengeti National Park but also other surrounding conservation areas. The general trend is for the land to receive less and less rain per year as one moves from the northwest to the southeast.

illustration in today's world of the way water can exert a dominant controlling effect on biological processes in an ecosystem.⁴

In the Serengeti, there is a gradient of decreasing moisture availability (increasing aridity) from the northwest to the southeast because of the positions of mountains and highlands, the directions of winds, and the courses followed by rivers; total annual rainfall in the northwest (~110 cm/year) is about twice that in the southeast (~50 cm/year). In the rainy season, enough rain falls everywhere for lush growth of grasses. However, during the long dry season between June and November, the southeastern plains typically receive almost no rain. As the dry season progresses, streams and rivers in the southeast first stop flowing, and they become nothing but a series of puddles and ponds. Then even the puddles and ponds dry up. The soil becomes parched, and the grasses turn brown and brittle. These seasonal patterns set the stage for the annual migration.

Not all species of large herbivores participate in the migration. In fact, most of the drinking-water-independent species do not. Grant's gazelles, elands, dik-diks, and most other drinking-water-independent species simply "stay put," even as the thronging herds of migrating animals move through. The most abundant migratory species is the wildebeest, which in recent times has numbered about 1 million. Another highly visible migratory species is the zebra. Both the wildebeest and zebra are drinking-water-dependent. They spend the dry season in the far northwest (Figure 30.4a). Then, as the rainy season starts in November or December, they move on a broad front from the northwest toward the southeastern plains

(Figure 30.4b). While the rains fall in the southeast (Figure 30.4c), they find water and lush grass there. However, after the rains stop in the southeast during the following May or June, they must get out of the area. First they move west (Figure 30.4d), and then—as the landscape becomes ever drier—they move in thundering herds back to the far northwest (Figure 30.4e), where they have the best chance of finding the water they require during the season of little rain. As we discussed in Chapter 6 (see page 135), scientists have only hypotheses—not certain knowledge—about why wildebeests and zebras move from the northwest to the southeast when the rainy season arrives. However, there can be no doubt why these animals leave the southeast when the rains stop: They need to drink each day, and doing so in the southeast becomes impossible. Meanwhile, drinking-water-independent species are free to stay put or make just relatively subtle adjustments to the strong seasonality of water availability.

Although the Serengeti migration seems almost unique today, it was not unique primordially. Migratory herds evolved in other settings as well. For example, wildebeests in the large Kalahari ecosystem at the border of Botswana and South Africa used to migrate in much the same pattern as those in the Serengeti. Most of these other migrations have been ended by human intervention. The Kalahari migration, for instance, was disrupted by fences and

⁴Recall Imanuel Noy-Meir's famous definition of a desert, mentioned at the start of this chapter.

the installation of wells, which the wildebeests congregate around rather than migrating to seek water.

Carnivorous mammals such as lions and cheetahs are generally assumed (on the basis of little evidence) to achieve water balance without having to drink much (if at all) because of the high water content of their foods. Some predators in the Serengeti are indifferent to the migration, whereas others follow the prey animals.

Water conflicts threaten animals and people

Water conflicts seem to be almost inevitable, as well as intrinsically ominous, in ecosystems where water exerts dominant controlling effects on biological processes. The conflicts that presently exist are worth noting because they threaten the future existence of the species and systems of life we are discussing.

One sort of water conflict is that between the water needs of desert and dry-savanna ecosystems and the water claims of human enterprises outside the ecosystems. In the United States, burgeoning cities in arid parts of the West and equally burgeoning demands for agricultural irrigation water have led to the draining and diversion of many of the rivers that once flowed through the western deserts and savanna-like prairies. A dramatic example is provided by the Colorado River, which is tapped for so many human uses as it flows from the Rocky Mountains to the Sea of Cortez (Gulf of California) that in many years it now runs out of water before reaching its ancient destination and dries up in the desert. Near the northern boundary of the Serengeti ecosystem, several actual or proposed human ventures pose threats of water conflict with the wildlife. The drinking-water-dependent species in the ecosystem, as we have seen, rely on a dependable supply of drinking water in the northwest to survive the dry season. The sufficiency of this supply is already less than fully adequate; during drought years, 20–30% of the wildebeest have been known to die. The principal reliable water source in the northwest is the Mara River, which brings water into the Serengeti ecosystem from forested highlands farther north. Deforestation of the highlands, diversion of river flow for irrigation uses, and diversion for hydroelectric power production have been proposed. All could create water conflicts with the wild animals in their dry-season refuge, potentially disrupting the migration and the entire Serengeti ecosystem.

Another major sort of water conflict arises from the traditional lifestyles of indigenous peoples living within desert and dry-savanna ecosystems. Throughout the world, the traditional way of life for hundreds of cultural groups in such places was nomadism. The indigenous people survived on very small amounts of water compared with modern urban water usage (Table 30.1), and they obtained the water they needed by moving with the rains. As notions of private land ownership spread around the world in the last few centuries, such ways of life became threatened or were eliminated because private land ownership is not readily compatible with nomadism; a nomad today would be encroaching on one piece of private property after another. Thus, as we look at a modern-day Maasai (Figure 30.5) or modern-day representative of any other nomadic group, we see two things. First we are reminded of the peoples—not just the wild animals—that lived for millennia in the deserts and dry savannas, integrated with these places in their natural state. Second, we see the troubled ending of a way of life as modern governments impose changed relationships to the land and, importantly, to water. Many nomadic peoples have been



FIGURE 30.5 A Maasai youth of college age He is a member of the current generation of a people who until recent times were nomadic in the dry savannas of East Africa.

settled on their own private parcels of land, but in the deserts and dry savannas, a single parcel is unlikely to provide adequate water through all years and all seasons; the people used to be nomads precisely because movement was necessary.

A debate that today has reached its time of ultimate resolution is whether some nomadic cultures should be given a chance to continue by protecting large tracts of land for nomadic use or even by assimilating the people into parks now reserved exclusively for wild animals. The challenges are particularly acute for the herding cultures, whose herds of cattle or goats traditionally provided them with a way to glean the essentials of life from the arid land, but today greatly magnify water conflicts. Protected parks for wild animals in deserts and dry savannas have nearly always had their borders set to include the most reliable water sources. When the herds kept by nomadic peoples are banned from the parks, the herds are kept

TABLE 30.1 Water use by people in four sorts of communities in Arabia

People in indigenous desert settlements use one-tenth the water of people in modern towns. The figures are for all domestic water use, including drinking, washing, bathing, and other water demands.

Type of community	Domestic water use per person (L/day)
Modern Arabian town without major industry ^a	240
Traditional agricultural village	120
Small desert settlement with supply by government water truck	80
Small desert settlement with traditional water supply	28

Source: After Goudie and Wilkinson 1977.

^aNew York City has a similar usage rate.

from the most dependable places to drink, but when the herds are let into the parks, they compete with the wild animals for water.

All species of large herbivores require considerable amounts of preformed water

Let's now take a more quantitative approach to understanding the water physiology of oryxes, gazelles, wildebeests, and the other large wild herbivores of deserts and dry savannas. Recall that under many conditions, kangaroo rats and other small desert rodents get well over half their water as metabolic water; at 25°C, for example, up to 90% of a kangaroo rat's water needs are met by metabolic water (see Figure 28.24). In sharp contrast, *all the species of large herbivores of deserts and dry savannas acquire most of their water as preformed water*.

To see this more clearly, let's consider the water budgets of two very different mammals of similar body size: the highly drinking-water-dependent common wildebeest and the highly drinking-water-independent beisa oryx. These animals were studied under two sets of conditions. The first set of conditions was designed to be about as mild as the animals would ever experience in nature; the environmental temperature was kept constantly at about 22°C. The second set of conditions was intended to simulate more closely the high water stresses the animals sometimes encounter; during each 24-h day, the temperature was raised to 40°C (104°F) (simulating daytime heat) for 12 h and lowered to 22°C (simulating night) for the other 12 h. Under both sets of conditions, the animals were gradually given less and less preformed water per day until they reached the minimum they required to maintain health. They were then maintained on that minimum for 2 weeks so that their water budgets could be studied.

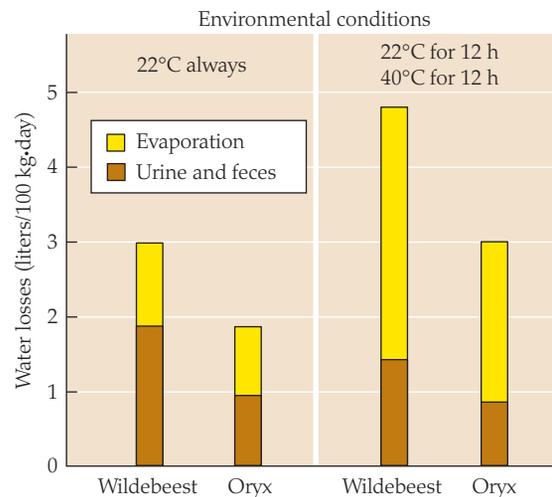
The results (Figure 30.6) reveal that the drinking-water-dependent wildebeest has a far greater total water need, and a far greater need for preformed water, than the drinking-water-independent oryx when both species are studied side by side under identical conditions. Physiologically, the two species are dramatically different.

A second major insight revealed by the results, however, is that even the oryx—which is famous for being one of the most drinking-water-independent of all large mammals—requires considerable quantities of preformed water to stay in water balance. Metabolic water met only about 20% of the oryx's total water need under both sets of conditions (see Figure 30.6b). Preformed water, therefore, had to meet about 80% of its need. How is it possible for a species to be drinking-water-independent yet require preformed water to meet much of its daily water requirement? The answer is that the oryx must meet much of its daily water need using preformed water *in its foods*.

In their water budgets, the wildebeest and oryx are quite typical of the large herbivores that live in deserts and dry savannas. Keeping the data on the wildebeest and oryx in mind (see Figure 30.6), we can make the following key points about the large herbivores as a group:

- All the species of large herbivores depend more on preformed water than on metabolic water to meet their water needs.
- Drinking-water-dependent species cannot get all the preformed water they need from their foods, either because they need more preformed water than available foods could ever provide or because they are ineffective in selecting and processing foods to maximize their acquisition of preformed

(a) Water losses



(b) Water gains

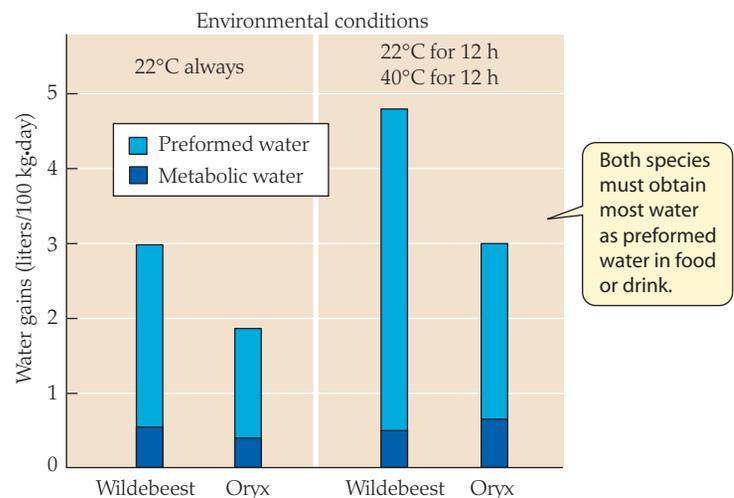


FIGURE 30.6 Water budgets of wildebeests and oryxes The wildebeests (*Connochaetes taurinus*) that were studied averaged 160 kg in body weight; the oryxes (*Oryx beisa*) were about the same weight, averaging 100 kg. The two species were studied in identical chambers that permitted their water losses (a) and gains (b) to be quantified. During some experiments (left) the air temperature was a constant 22°C. During others (right) the air temperature was 22°C for half of each 24-h day and 40°C for the other half. The animals had been acclimated to water restriction before the start of these measurements and were maintained on water restriction throughout the study. (After Taylor 1968, 1970.)

water. Therefore, they have to drink each day for their total intake of preformed water to be adequate to keep them healthy.

- Drinking-water-independent species, in contrast, can get all the preformed water they need to stay healthy—for many days in a row—from their foods. This is why they are classed as drinking-water-independent; it is why they do not require drinking water very often. This said, it is important to note that obtaining adequate preformed water from foods is far from simple, as we will soon see, because the foods available in deserts and dry savannas are often parched.

- Most drinking-water-independent species in fact need to drink occasionally during the hot-dry seasons of the year. Although the preformed water they get from their foods is *almost* enough to meet their total need for preformed water, it is not *fully* adequate. Thus, when they do not drink on a given day, they become a bit dehydrated. They become a bit more dehydrated the next day, and so forth, until ultimately—after a week or two (or longer)—they need to find drinking water.
- A few drinking-water-independent species are believed to be able to meet their entire need for preformed water from the preformed water in their foods even in the hot-dry seasons of the year, meaning that they need never drink. The oryx and eland are often cited as examples. Field biologists report that these species are never observed to drink in water-poor regions. Moreover, physiological data (which we will soon discuss) make it plausible to believe that these animals acquire enough preformed water from their foods that they never require drinking water.

Water and food resources in the deserts and dry savannas are often complex

Now that we have addressed the needs of large herbivores for preformed water in drink or food, a next logical step is to consider the nature of the drinking-water and food resources available to them. These resources are often far more complex in their properties than meets the eye.

One complexity in both deserts and dry savannas is that *when standing water is found, it is often salty water*. Recent measurements have revealed, for example, that in the central and southeastern Serengeti ecosystem, salinities of 5–15 g/kg are common in the headwaters of major rivers, and salinities of 20–30 g/kg (approaching equality with seawater) are common in stagnant pools or landlocked lakes. Not all Serengeti waters are this salty; some have salinities lower than 1 g/kg. Nonetheless, one cannot help but be impressed with how salty the waters can be in this benign-looking grassland ecosystem. Some investigators postulate, in fact, that the immediate stimulus for the migrating herds to leave the southeast Serengeti at the end of the rainy season is the increasing salinity of the drinking water as the landscape dries.

Why are waters in deserts and dry savannas so often salty? Briefly speaking, soils in arid regions are commonly salty, and the waters become salty by dissolving salts out of the soils. A key reason the soils are salty is that they get so little rain that they are rarely thoroughly flushed with water. Typically, each rain brings a trace of salt with it.⁵ When the rain hits the ground in arid regions, it soaks in to only a shallow depth and evaporates. Rain after rain causes salts to build up incrementally in the upper layers of the soil. These salts then dissolve into any pools of water that form on top of the soil, making the water salty until it itself evaporates, leaving the salts behind once more. This process is accentuated in low places where rain tends to settle in pools or flow in temporary streams. In such places, particularly large amounts of water accumulate after each rain and leave particularly large quantities of salts behind after evaporating.

⁵Aerosolized seawater can be detected in tiny amounts in the atmosphere hundreds of miles inland from the oceans, for example. The salts dissolve in cloud droplets and are carried to Earth in rain.

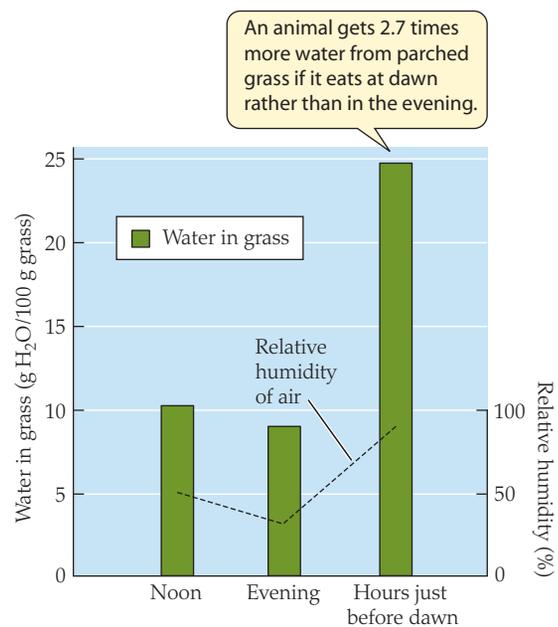


FIGURE 30.7 The moisture content of “dry” grass varies with time of day or night. Data were gathered on dead, brown blades of the perennial desert grass *Stipagrostis uniplumus* in the Namib Desert. The water content of the grass is highest near dawn, when the relative humidity is highest. (After Louw 1972.)

When animals find salty water to drink, their kidneys must be able to excrete each ion in the water at a higher concentration than in the water itself if the animals are to gain H₂O by drinking the water (see page 709). Thus the evolution of kidneys with exceptional concentrating abilities has been important for desert and savanna mammals *both* because a high concentrating ability allows ordinary soluble wastes to be excreted with relatively little water *and* because it permits animals to gain H₂O from saltier water sources than would otherwise be acceptable. Despite kidney specializations, when drinking waters approach half the concentration of seawater, they cease being useful H₂O sources for some of the species of mammals that are native to the deserts and dry savannas.

A second important complexity of water and food resources in deserts and dry savannas is that *in dry seasons, the leaves of plants often undergo large and rapid swings in their content of preformed water because of equilibration with the humidity of the air*. When this phenomenon was first reported about 40 years ago, it seemed that it might be merely a footnote in the biology of a few species. By now, however, desert biologists recognize the phenomenon as being often of extreme significance in the water biology of large herbivores. **Figure 30.7** shows how a perennial grass that is a favored food of herbivores varies in its moisture content because of equilibration with changing atmospheric humidity between midday, evening, and the dark hours before dawn in the Namib Desert. The measurements were made in the dry season, when the blades of the grass were dead and brown. Although ostensibly “dry” all the time, dead grass blades quickly equilibrate with changes in atmospheric humidity and have a far higher water content at the end of the night than at midday or evening. Accordingly, animals can increase their input of preformed water by eating preferentially in the hours around dawn, and research has shown that many species do.

A third aspect of the complexity of water and food resources has both obvious and less obvious aspects. In deserts and dry savannas, *both the growth and the nutritional composition of plants tend to be highly*

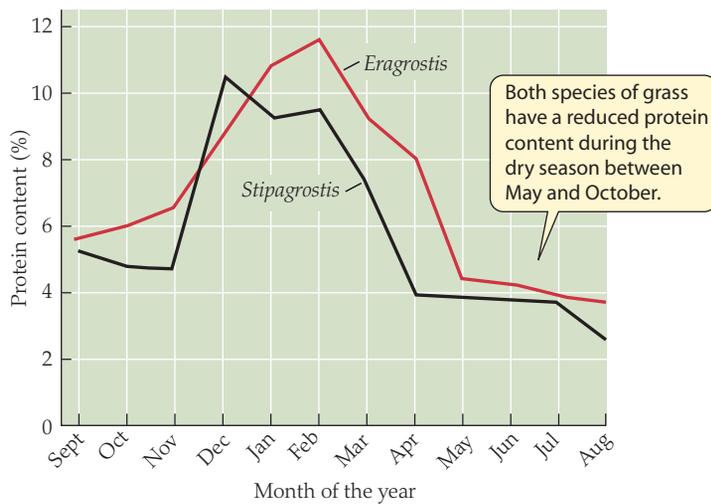


FIGURE 30.8 The nutritional content of some plants varies with rainy and dry seasons The percentage of protein in two species of perennial grasses (*Eragrostis lehmanniana* and *Stipagrostis obtusa*) eaten by wildebeests and oryxes was measured throughout the year in the southern Kalahari Desert ecosystem. (After Lovegrove 1993.)

correlated with changes in water availability. The effects of rainfall on plant growth are obvious: In deserts, where rainfall occurs irregularly and unpredictably, plant growth is likewise irregular and unpredictable. In savannas, plant growth waxes in the wet season and wanes in the dry season. What is not obvious is that some plants vary markedly in their content of nutritionally important materials as rains come and go. Certain of the important perennial grasses in the Kalahari Desert ecosystem, for example, vary dramatically in their protein content between the wet and dry seasons (Figure 30.8).⁶ A recent study of grasses in a hyperarid Arabian desert showed that protein content (computed relative to plant dry weight) falls exponentially during long periods of drought, from about 9% in the early weeks of drought (just after the cessation of rain) to 5% a year later. After long periods of drought, the concentrations of phosphorus, copper, and other minerals are sometimes too low in desert plants to meet the nutritional needs of herbivores.

A final aspect of the complexity of water and food resources is the formation of fog and the deposition of fog water on plants and other objects. Fog and fog water are potentially significant sources of water in deserts or savannas located within about 80 km of sea-coasts, particularly coasts where—because of upwelling or other oceanographic processes—there is a narrow band of cold seawater along the shore. Fogs often recur so frequently in such places that they can make a major contribution to the ecosystem water budget. Although several mechanisms of fog formation are likely, the most common is that warm moist air blowing landward from the open ocean is cooled just before making landfall by passing across the cold coastal band of water, and this cooling of the air causes its saturation vapor pressure to decline (see Table 27.2), forcing water out of the vapor state to form fog droplets. In hyperarid coastal regions that have frequent fogs—such as parts of the deserts in Namibia, Chile, and Oman—there is so little rainfall and so much fog that plants may receive several times more water by deposition of fog water on their surfaces than they receive from rain! Some desert arthropods, such as certain beetles and scorpions, are specialists in gathering

⁶The leaves and seed pods of Kalahari trees, however, do not show such strong seasonal changes.



FIGURE 30.9 The desert beetle *Onymacris unguicularis* collects water from fog in the Namib Desert When fog rolls in from the sea, as it does often because of local conditions, the beetle goes to the crests of sand dunes and positions itself, as shown, in a “fog-basking” stance, in which its broad dorsal surface faces into the fog-laden sea-breeze. As the fog water accumulates on the beetle’s body, the water runs down to the beetle’s mouth.

the fog water (Figure 30.9). For the large desert herbivores that are our focus in this chapter, the effects of fog are more indirect: Fogs provide water to the plants that these herbivores eat. This input of water not only increases the water content of the plants but helps maintain plant health, so that—for example—plant protein stays higher than it otherwise would, making the plants more nutritious.

The Dramatic Adaptations of Particular Species

For the most part, the physiologists who have made the effort to study the large mammals of deserts and dry savannas have been water-balance specialists. It’s a commentary on human nature, rather than animal nature, that scientists—like all people—have personal proclivities that lead them to attach greater importance to some things they observe than to others. Water-balance physiologists tend to attach greatest importance to adaptations that permit animals to live with as little water as possible. With water-balance physiologists organizing most physiological research in the deserts and dry savannas, wildebeests—noted for their slavish dependence on sources of drinking water—have often been dismissed as uninteresting.

Before we turn to the “water-balance champions”—species famed for extreme degrees of independence from drinking water—we would do well to pause a moment to recognize how remarkably successful wildebeests are. Here is a stunning fact: In the Serengeti, wildebeests outnumber all the other species of large mammals combined! This is true even though they are noted more for needing water than for conserving it. Faced with life in an environment that dries out for months at a time, instead of evolving exceptional modes of surviving without drinking water, wildebeests have evolved ways of getting themselves reliably to places where they can find the drinking water they need. If wildebeests have extraordinary adaptations, their special abilities probably reside in their brains

and sense organs, which physiologists other than water-balance physiologists will ultimately study. Clearly wildebeests are able to *navigate* during their long migratory treks each year. They probably have other exceptional nervous system abilities as well. Naturalists report, for example, that wildebeests in the northwestern Serengeti often start moving southeast at the start of the rainy season before rain is actually falling in the northwest. Do they hear distant thunder or smell distant rain and respond by moving out across a mental map? The answers cannot help but be fascinating.

Let's now discuss four case studies of the sort that intrigue water-balance physiologists: the cases of the oryxes, the Thomson's and Grant's gazelles, the sand gazelle, and the dromedary (one-humped) camel. These are all large animals that, because of their size, have limited opportunities to find protective microenvironments. Consequently, when they live in hot, dry environments, they often actually experience heat stress during all the hours it prevails, and they therefore confront directly the fundamental conflict between heat balance and water balance: Although use of water for evaporative cooling provides a *physically straightforward* way to rid the body of excess heat, it is not *ecologically straightforward* when environmental water is in short supply. We saw earlier that large body size is a physiological advantage in hot, dry environments (see Figure 30.1). Large size in itself, however, does not permit an animal to be completely independent of drinking water in deserts and dry savannas. All of these animals have evolved exceptional species-specific adaptations for maintaining water balance in places where water exerts a dominant controlling effect on life.

Oryxes represent the pinnacle of desert survival

Among the truly wild large mammals, oryxes (Figure 30.10) represent the pinnacle of evolution in their ability to survive in deserts. Dromedaries might be their equal physiologically, but wild dromedaries went extinct before historical times, and today's dromedaries are either domesticated or escaped from domestication. Four types of oryxes are recognized, although taxonomists debate whether some are species or subspecies. The three types that have featured in physiological research are the gemsbok oryx (*Oryx gazella*) and beisa oryx (*O. beisa*)—which closely resemble each other—and the Arabian oryx (*O. leucoryx*). The Arabian oryx, a species that weighs 70–100 kg, was driven to extinction in the wild for a time but has been reestablished. Oryxes can live in some of the most inhospitable places on Earth—including hyperarid deserts where summer air temperatures sometimes exceed 45°C (113°F), the sun shines inexorably, there is no drinking water except immediately after rains, and the rains themselves are so infrequent that average precipitation is less than 5 cm (2 inches) per year.

A decade ago, researchers measured the total water turnover rates of *free-living* Arabian oryxes by use of isotopically labeled water (see page 743). They found the water turnover rates of the oryxes to be only one-quarter to one-half as high as would be expected for free-living mammals of their body size. The same team also measured evaporative water loss in *caged* Arabian oryxes. They found that as oryxes are acclimated to water restriction, they conserve water better: They reduce their metabolic rate (lowering respiratory evaporation), lower their total rate of evaporative water loss so it is only about half as high as in nonacclimated oryxes, and achieve a total rate of evaporative water loss that is only 40%



FIGURE 30.10 Oryxes in deserts often exist on dead, dry grasses and the leaves of water-stressed bushes and trees Oryxes are able to stay in water balance with their only preformed water coming from such sources because they conserve water exceptionally well by mechanisms that are only partly understood. The animal shown is a gemsbok (*Oryx gazella*).

as high as expected for ungulates of their body size studied under caged conditions. These recent results confirm the conclusion reached by the earlier laboratory studies we discussed (see Figure 30.6) that oryxes have evolved unusually low water needs. Oryxes are far more effective than average mammals of their body size in limiting their rates of water loss and, therefore, the rates at which they must resupply themselves with water.

The *mechanisms* by which oryxes achieve exceptional water conservation and low water-turnover rates are only starting to be understood. The kidneys of beisa and Arabian oryxes can concentrate urine to an osmotic urine-to-plasma (U/P) ratio of about 8 (Table 30.2)—a high value for animals of their size (see Figure 28.20). Free-living Arabian oryxes lower their metabolic rates in summer to be only half as high as in winter, based on doubly labeled water studies (see page 208). Although oryxes are famous for being indifferent to shade under many circumstances, they methodically remain inactive in shade—if they can find it—during the heat of the day when under water stress. At least two species sometimes dig shallow depressions in which they settle down; this behavior is thought, without evidence, to shield them from the sun or allow them to lose heat to the cool subsoil they expose. Pregnancy and lactation place substantial water demands on females, and a recent study indicates that in Arabian oryxes, reproduction is curtailed during drought; both mating behaviors and conceptions were only about 20% as high during a dry year as during a moist year.

The water-conserving mechanism that is now best understood in oryxes—and thought generally to be widely used by other desert and dry-savanna species—is modulation of body temperature in ways that minimize the use of water for thermoregulation (see pages 260–261). A person placed in a hot desert maintains a stable body-core temperature of about 37°C, but at the price of profuse sweating, which entails rapid water loss (up to 2L/h). Oryxes and other species of large mammals with long evolutionary histories in

TABLE 30.2 Maximum urine concentrations and minimum fecal water concentrations in selected African mammals

All values are from dehydrated animals.

Species	Urine osmotic pressure (mosmol/kg H ₂ O)	Osmotic U/P ratio ^a	Fecal water content (g H ₂ O/100 g)
African buffalo (<i>Syncerus caffer</i>)	1120	4	
Hereford cow (<i>Bos taurus</i>)	1160	4	75
Zebu cow (<i>Bos indicus</i>)	1300	4	
Somali donkey (<i>Equus asinus</i>)	1680	5	61
Common wildebeest (<i>Connochaetes taurinus</i>)	1830	6	
Thomson's gazelle (<i>Gazella thomsoni</i>)	2640	7	
Arabian oryx (<i>Oryx leucoryx</i>)	2500	8	43
Beisa oryx (<i>Oryx beisa</i>)	3100	8	
Grant's gazelle (<i>Gazella granti</i>)	2790	8	
Dromedary camel (<i>Camelus dromedarius</i>)	3200	8	44
Dik-dik (<i>Madoqua kirkii</i>)	4760	~12	44

Sources: After Maloij et al. 1979; Ostrowski et al. 2006; dik-dik urine data updated from Beuchat 1996.

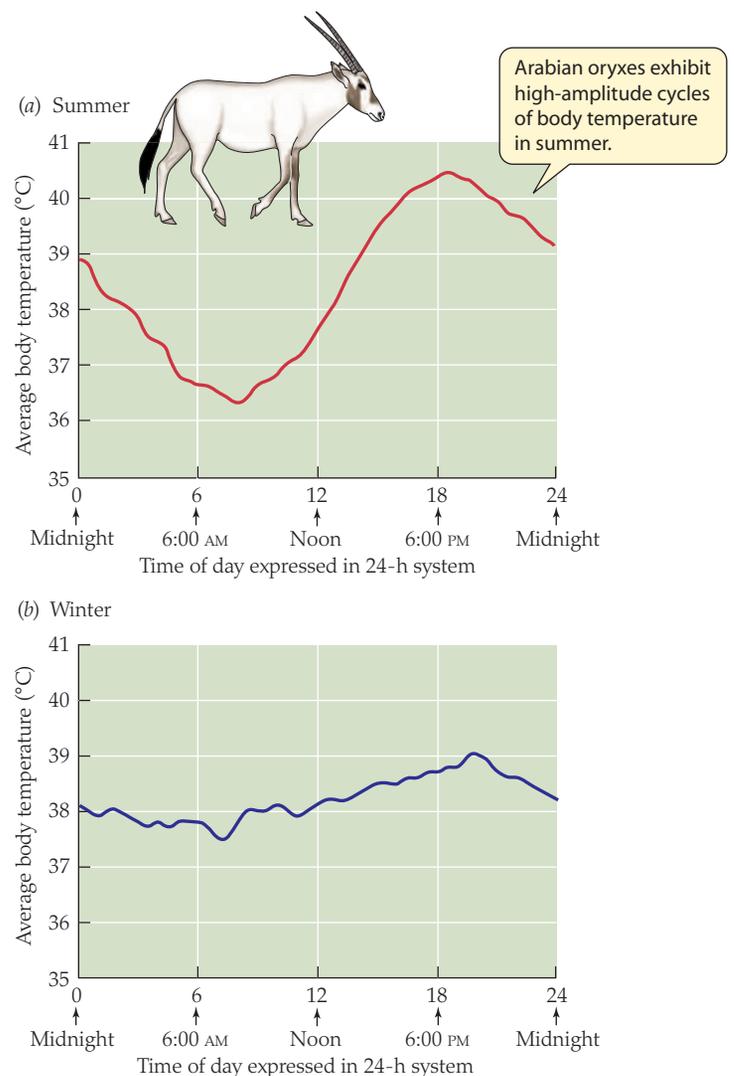
^aU/P ratios depend in part on plasma values, explaining why they do not always correlate exactly with urine osmotic pressures.

hot-dry environments are hypothesized in general to exploit the advantages of a *variable* body-core temperature when necessary to save water. The firmest supporting evidence for this hypothesis available today in any species is in fact provided by two recent studies of Arabian oryxes living wild in the deserts of Saudi Arabia. The body temperatures of the animals were monitored remotely for hundreds or thousands of hours by use of radiotelemetry in one study and by data loggers⁷ in the other. The results of one study are presented in **Figure 30.11**. The average body-core temperature rose and fell to a small extent over the 24-h day during winter (see **Figure 30.11b**), when the ambient air temperature varied from an average low of 13°C at night to an average high of 27°C during the day. In summer, however, when the ambient air temperature varied from a nighttime low of 29°C to a daytime high of 44°C (111°F), the amplitude of the oryxes' cycle of body-core temperature became much larger (see **Figure 30.11a**). On average, the oryxes in summer let their body temperatures fall to 36.5°C overnight, but then rise to 40.5°C during the day: an average amplitude of about 4°C. The second, completely independent study on Arabian oryxes obtained similar results; the average amplitude in summer was 5°C. In the two studies taken together, three individuals were observed at times to allow their body-core temperature to cycle by 7.5–7.7°C between night and day—the highest amplitude daily cycle ever observed in any mammal.

The oryxes' high-amplitude cycles of body temperature are believed to save water in two ways (see pages 260–261). First, when

⁷Data loggers are devices that, as they collect data, log the data into digital memory. They are later recovered and the data downloaded.

FIGURE 30.11 Average body-core temperatures of free-living Arabian oryxes over the 24-h day The six oryxes (*Oryx leucoryx*) studied were living in their natural environment in Saudi Arabia and monitored using implanted radiotelemeters during (a) summer and (b) winter. (After Ostrowski et al. 2003.)



the animals let their body temperatures rise during the heat of the day, they are in effect *storing* heat instead of panting or sweating to get rid of it. They then exploit the coolness of the nighttime environment to lose the heat by nonevaporative means (convection and thermal radiation). The water savings per day from allowing the body temperature to cycle—rather than holding it constant by panting or sweating—is about 0.3–0.4 L for an oryx of average size. The elevation of body temperature during the day also has a second advantage: It *reduces the difference in temperature between an oryx's tissues and the hot environment during the heat of the day*, thereby slowing the rate at which heat enters its body.

Remote-monitoring techniques—such as radiotelemetry and automated data collection by data loggers—have only recently started to be used to study the physiology of desert and dry-savanna mammals, and only three studies have been completed on the body temperatures of free-living oryxes (none has been completed on free-living camels or gazelles). Two of the studies are those we have just discussed. The third study did not find large cycles of body temperature in the oryxes monitored (*O. gazella*). This may mean only that the animals were not experiencing a tendency to dehydrate. Many laboratory investigations have demonstrated that desert and dry-savanna mammals are in general far more likely to allow large swings in body temperature when they are tending to dehydrate than otherwise. Moreover, one of the studies on free-living Arabian oryxes found a correlation between the amplitude of body temperature cycles and environmental moisture: The cycles became greater as the environment became drier. A goal for physiologists as they make greater use of remote-monitoring techniques will be to understand better how free-living animals modulate their use of the water-conserving mechanisms they possess.

Up to now we have discussed just one side of the water-balance equation in oryxes: their ability to limit water losses. What about water gains? Studies on free-living oryxes in the wild confirm that, as laboratory data suggest (see Figure 30.6), they must meet most of their water needs with preformed water. Metabolic water can account for only one-quarter or less of their water inputs in the wild.

Although oryxes drink when they find water and are even known at times to dig for water in riverbeds, there can be no doubt that they often live for months or even years without drinking. They then get the preformed water they need from their foods—an astounding proposition, because the foods available to them often seem to the eye to be distinctly unpromising. Oryxes eat the leaves of desert trees, such as acacia trees. These leaves, although they are firm and not ostensibly juicy, turn out, when analyzed, to be at least 50–60% water, even in the midst of severe droughts. Oryxes also eat dried grasses and other dead, dry plants (see Figure 30.10), and when they do so, they time their feeding to occur principally in the predawn hours, when the plants are richest in water (see Figure 30.7). In dry times, oryxes become nomads in the deserts, seeking out places where fog, dew, or rain has allowed plants to build up more water than average. According to some orthodox scientific evidence plus reports of the San people, who have lived in African deserts and dry savannas for millennia, oryxes have uncanny abilities to find and excavate the underground dormancy organs of desert plants, structures that can be 1 m deep but contain 50–70% water. All these strategies used by oryxes to obtain preformed water from food seem so marginal that they might not work to sustain life, and in fact there is no quantitative proof that they do work.

However, they apparently must work, because the oryxes survive. One reason life is possible on such meager water resources is water conservation. Surviving on the water in the leaves of water-stressed or dead plants would be impossible without mechanisms that can profoundly limit the amount of water an animal needs.

Oryxes have been recorded to survive rainless droughts in the desert for at least 34 months. Sometimes their body condition declines under such extreme duress, and some die. Even after 2–3 years without drinking, however, the problem that undermines oryxes seems most likely *not* to be dehydration, based on studies of recently dead animals. Instead, they seem most likely to die of severe protein deficiency (or other nutritional deficiency) caused by the deteriorating nutritional quality of the plants in their environment.

Grant's and Thomson's gazelles differ in their relations to water

Grant's gazelle (*Gazella granti*) and Thomson's gazelle (*G. thomsoni*) are two look-alike antelopes, weighing 10–50 kg, that often coexist in abundance in the savannas of East Africa (see Figure 30.3). Both are drinking-water-independent⁸ and often stand in the open all day long, indifferent to shade. For five decades the contrasts between these two species have highlighted that straightforward studies of water input and water output do not always tell the entire story about the water relations of savanna animals.

When Grant's and Thomson's gazelles are subjected to standard water-balance analyses in laboratory settings, they prove to be similar. If anything, Thomson's gazelle seems more adept at conserving water during such tests. However, in their natural environment, the species clearly have different relations to water, and of the two, Thomson's gazelle paradoxically seems to be the inferior one in coping with water stress. In the Serengeti, Thomson's gazelles participate in the annual migration; despite being drinking-water-independent, they trek along in great numbers with the drinking-water-dependent wildebeests and zebras. Where savannas give way to deserts, although Grant's gazelles occupy the deserts as well as the savannas, Thomson's gazelles stay largely in the moister savannas.

The study of physiology has yet to explain the divergence of the water relations of these two gazelle species in the wild. Some insight is probably provided by their different responses to extreme ambient temperatures in laboratory tests. Exposed to an air temperature of 45°C, Grant's gazelle allows its body temperature to rise to 45°C or higher; some individuals reach a rectal temperature of 46.5°C (116°F), among the highest ever recorded in a vertebrate. Thomson's gazelle, however, keeps its body temperature below 43°C, a process that means more panting and more use of water for thermoregulation. The two species may also differ in food selection (the plants they select to eat and the times when they eat them), behavioral thermoregulation, or other traits that only careful field studies will bring fully to light.

The sand gazelle is drinking-water-independent in hyperarid deserts

The sand gazelle (*Gazella subgutturosa*), which weighs about 20 kg and therefore is similar in size to Grant's and Thomson's gazelles,

⁸Recall that “drinking-water-independent” is a category of drinking behavior. Drinking-water-independent species do not need to drink each day but can skip drinking for many days or weeks in a row. They may not, however, be entirely independent of drinking water.



FIGURE 30.12 Dromedary camels—the “ships of the desert”—do not carry extra water in their bodies, as legend has often held. Instead, they depend on water conservation, an ability to eat diverse desert foods, and extreme tolerance of dehydration to be able to go for days or weeks without drinking. They have a long history of use as beasts of burden in much of northern Africa and southern Asia and have been imported into Australia. They are the largest of the mammals adapted to desert life, sometimes reaching adult weights of 500–600 kg.

dramatically illustrates the physiological diversification that can occur within sets of closely related animals (in this case three species in the single genus *Gazella*). The sand gazelle lives in full-fledged deserts, including hyperarid deserts, and therefore—averaged over the course of an entire year—tends to face greater problems of water availability than savanna-dwelling Grant’s and Thomson’s gazelles. Recent research has revealed that the sand gazelle has evolved a strikingly low rate of evaporative water loss (EWL). Its total EWL is only about 20% as high as the EWL of Grant’s or Thomson’s gazelles—and also only about 20% as high as expected for an average ungulate of its body size. The mechanisms by which EWL is so profoundly reduced remain to be fully understood. Two mechanisms documented thus far are cycling of body temperature (summer amplitude: 2.6°C) and a reduction of metabolic rate by as much as 45% when acclimated to food and water restriction.

The dromedary camel does not store water, but conserves it and tolerates profound dehydration

The modern era of physiological research on large desert mammals began with studies on dromedary camels (Figure 30.12) by Knut and Bodil Schmidt-Nielsen in the mid-twentieth century. More has steadily been learned since then. Dromedaries drink, in part because they are domesticated and their human handlers

water them. Nonetheless, they are capable of extreme performance in some of the most inhospitable places. During the cool seasons of the year, for example, dromedaries are able to travel for several weeks and cover hundreds of desert miles—serving as beasts of burden—without drinking along the way.

From the time of ancient Rome until the Schmidt-Nielsens’ pioneering studies, the reigning theory about the camels’ low requirement for drinking water was that they had a canteen onboard. That is, people assumed that camels have a greater amount of body water than ordinary mammals when they start a trek. For centuries, debate therefore focused on the location of the canteen, with most commentators supposing that the rumen or parts of the rumen played this role. After early biochemists established that water is made by metabolism, even the hump became a proposed site of canteen function. Not that the hump contains water: Scientists have long recognized that the hump is filled with fat. However, fat yields more than its own weight in H₂O when it is oxidized (see Table 27.3), and thus it seemed only logical that the fat in the hump was a lightweight way to carry H₂O. The Schmidt-Nielsens and later investigators systematically demolished all these myths, some of which had “provided the answer to the camel question” for 2000 years. A camel’s rumen contains no more water than any other ruminant’s rumen. When the total amount of water in a camel’s body is measured, it is no more than the average for all mammals. The hump fat actually *costs* H₂O to oxidize because the H₂O lost in breathing to obtain O₂ for the oxidation of the fat exceeds the metabolic water produced (see page 710). In the end, researchers established beyond doubt that camels drink only to make up for prior water losses, never to store water in their bodies in anticipation of future water needs.

There are two principal keys to the extraordinary ability of camels to survive in deserts for long periods without drinking. One of these

is by now a familiar theme: Camels conserve water extraordinarily well. Based on studies of penned animals, we know that dromedaries dramatically exploit the water-conservation benefits of large daily changes in body temperature. When dehydrated, they sometimes allow their body temperature to rise as much as 6°C during the day and fall to the same extent in the cool of night. One reason they can permit their body temperature to rise as high as it does is that they keep their brain cooler than the rest of their body (see page 261)—a trait also reported in oryxes and gazelles. Dromedaries also employ several other water conservation strategies: (1) they can produce dry feces and concentrated urine (see Table 30.2); (2) they curtail their urine production relatively rapidly and profoundly when faced with dehydration; (3) they have thick, sometimes glossy, fur that acts as a heat shield, helping to slow influx of heat from the fur surface and reflect or reradiate incoming solar radiation (see page 260); and (4) they minimize heat influx behaviorally, as by steadily facing the sun when allowed to rest during the day, a practice by which they consistently present a narrow body profile to the sun's direct rays.

The second known key to the ability of camels to survive for weeks without drinking water is their unusual tolerance of dehydration. Species of mammals without long evolutionary histories in deserts, such as dogs or horses, are in danger of death if they dehydrate by 10–15% of their body weight while under heat stress. Dromedaries, in contrast, can tolerate at least twice this extent of dehydration. There are known cases of dromedaries being alert and functional in the desert heat while dehydrated by 30–40% of their body weight.

Thus, when a dromedary sets off on a desert trek, it has the same amount of body water, in relation to its body size, as you or I. However, it dehydrates by a smaller percentage of its body weight per day because it conserves water exceptionally well, and it can tolerate a level of total dehydration at least twice what we can tolerate. Along the way it munches desert plants, ranging from green leaves to dried-out thorn bushes and saltbushes, replacing some of its water losses using preformed water from its food. Thus it can forestall its need to drink for many days in the summer and many weeks in the cool seasons.

Study Questions

1. What are the pros and cons of studying water physiology in the laboratory and in the field? Could an animal's water physiology be fully understood by field studies alone? By laboratory studies alone? Explain.
2. In Chapter 1 we noted that an animal's body size is one of its most important properties. Considering all the mammals that live in deserts, explain why their body sizes matter. Include discussion of physiological mechanisms where appropriate.
3. The effects of water loss in milk on the water budgets of lactating female mammals in arid environments are not well understood. Specify three hypotheses regarding mechanisms by which females might prevent water losses in their milk from forcing them into negative water balance (which could lead to fatal dehydration). For each hypothesis, design a study to test or evaluate the hypothesis.
4. Contrast the body-temperature responses of humans and Arabian oryxes during exposure to a hot-arid desert. In each case, state implications for water balance. Include both day and night in your analysis.

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See also **Additional References** and **Figure and Table Citations**.