

Seasonal patterns of water and energy balance in desert vertebrates

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Seven species of desert vertebrates living in winter-rainfall deserts were compared and contrasted with respect to the means they use to survive a year in the field. Each species appears to have a unique suite of survival mechanisms. Among the three herbivorous species, jackrabbits have the least-effective mechanisms for maintaining water and energy balance, many probably die after vegetation dries up during droughts, and populations are subsequently restored by rapid reproduction after winter rains. The two plant-eating reptiles, chuckwalla lizards and desert tortoises, both husband their water and energy budgets remarkably well, but chuckwallas have opted for precise osmotic and body fluid volume regulation, which restricts them to feeding only on green, moist vegetation in spring, whereas tortoises tolerate wide swings in their osmotic and fluid balance, and can thereby drink rainwater and eat dry vegetation during summer and autumn. Antelope ground squirrels conserve water and energy effectively, and they obtain adequate water and energy throughout the year without drinking, by varying their diet appropriately among arthropods, seeds and vegetation. Sand partridges and Chukar partridges do well from spring through early winter on their diet of seeds and green vegetation (supplemented by some arthropods for Chukars) primarily by drinking free-standing water during the warm season drought. These birds are apparently unable to obtain adequate energy from green vegetation which they consume after the winter rains cause their seed supply to germinate. Chukars survive this period by relying on stored fat, but Sand Partridges apparently migrate to warmer, drier areas. The insectivorous side-blotched lizards do not face a food quality problem because they eat water- and energy-rich animals, which are nearly continuously available due to the desert adaptations of these prey species. These seven species are not easily catalogued into one or a few patterns of desert adaptation. The substantial differences in the annual physiological ecology of the few desert animals studied so far suggests that a rich diversity of desert adaptations remains to be discovered.

Introduction

Lack of water is the most striking property of deserts, and water scarcity is the main challenge to survival faced by animals that live in deserts. However, even when a desert animal manages to obtain enough water, it may still face shortages of other nutrients, such as digestible energy and nitrogen. Because desert plant productivity is generally synchronized with seasonal rainfall patterns, vegetation is usually dry and of poor nutritional quality during drought seasons. Herbivorous animals often must deal with low food quality, whereas carnivorous animals may have to deal with low food quantity, because their herbivorous prey may become scarce during dry seasons.

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Seasonal patterns of water and energy availability differ among deserts. Winter-rainfall deserts, such as the Mojave in California and Nevada and the Negev in Israel, have drought conditions that occur during the hottest months of the year, whereas primarily summer-rainfall deserts, such as the Chihuahuan in Mexico and the Kalahari in southern Africa, experience dry winters. The nature of the tasks of maintaining water and energy balance differs in response to the timing of annual rainfall events in different deserts, with summer-drought deserts being perhaps relatively more challenging to resident animals. The seasonal patterns of water and energy metabolism in desert animals should be evaluated in context with the seasonality of their habitat, because nutrient availability has a major influence on the physiological performance of wild animals. Year-round field studies provide the most relevant information about survival mechanisms.

In this paper, I discuss seasonal aspects of the physiological ecology of seven species of desert vertebrates, all of which live in winter-rainfall deserts (five in the Mojave and two in the Negev). The animals are: the chuckwalla, *Sauromalus obesus* (a herbivorous lizard weighing about 170 g); the desert tortoise, *Gopherus agassizii* (a herbivorous reptile weighing 1–3 kg); the jackrabbit, *Lepus californicus* (a herbivorous mammal weighing 1.8 kg); the Antelope ground squirrel, *Ammospermophilus leucurus* (a 100-g omnivorous rodent); the Chukar Partridge, *Alectoris chukar* (a 500-g granivorous bird); the Sand Partridge, *Ammoperdix heyi* (a granivorous bird weighing about 200 g); and the side-blotched lizard *Uta stansburiana* (a 3-g insectivorous lizard). All species were studied using similar methods (see below). After summarizing the physiological ecology of these species, I address the question: Do these desert vertebrates fall into one or a few general patterns of surviving through a year? The best answer to date seems to be: No, each species does it differently.

Methods

Techniques for obtaining physiological and behavioral measurements on free-ranging animals in the field are being developed continually. Radio transmitters for telemetering information about location, activity level, temperature, respiration rate, cardiovascular variables and other physiological parameters are available (Mech, 1983). The use of stable and radioactive isotopes as tracers of physiological and ecological processes is increasing rapidly (Hendee, 1973; Klein & Klein, 1979; Fry & Sheer, 1984; Peterson *et al.*, 1985; Ambrose & DeNiro, 1986). The use of doubly labeled water (DLW) to measure energy and material balance in free-ranging animals (Lifson & McClintock, 1966; Nagy, 1980; Nagy & Costa, 1980) has mushroomed in the last decade. DLW works as follows: in an animal whose body water is labeled with an isotope of hydrogen (tritium or deuterium) and an isotope of oxygen (usually ^{18}O), the washout rate of the hydrogen isotope is a measure of water flux through the animal, and the washout of oxygen isotope reflects the sum of water loss and CO_2 loss (because the oxygen isotope is in equilibrium with, and hence traces, CO_2). The difference between hydrogen and oxygen isotope losses is a measure of CO_2 production, which is an indirect measure of energy metabolism. With information about diet composition and digestibility, DLW results can be used to estimate feeding rates (Nagy, 1975).

A combination of field and laboratory methods were used in the studies summarized below. Field metabolic rates, water influx and efflux rates, body mass changes, diets and seasonal patterns of behavior were determined in all cases. Laboratory measurements of digestibility of natural diets were also made on all species, and in some cases, itemized budgets for water, salt and nitrogen were determined during the feeding trials. More detailed studies of physiological capabilities (eg. salt gland, kidney and cloaca, and digestive tract function) have been made on some of these species.

Table 1. Checklist of adaptations that aid in maintaining water, salt and energy balance or enhance reproduction in seven species of desert vertebrates

Adaptation	Species						
	Chuckwalla lizard	Desert tortoise	Jack-rabbit	Ground squirrel	Chukar Partridge	Sand Partridge	Side-blotched lizard
Osmoregulatory physiology							
Plasma ion regulation	**		*	?	?	?	*
Fluid volume regulation	**		*	?	?	?	?
Low evaporative water loss	**	**	*	*	*	*	*
Dry feces	**	*	**	**	*	*	*
Dry or concentrated urine	**		*	*	?	?	*
Nasal salt glands	**						*
Storage of water		**					
Storage of salts		**					
Energy balance physiology							
Hyperthermia tolerance	NA	NA	*	**	*	*	NA
Estivation or torpor	**	**	*	*			*
Hibernation	**	**					
Fat storage	**	**	?	*	*	*	**
Behavior							
Diet selection	*	*	*	**	**	*	
Burrow use	*	**	*	**			**
Nocturnally active			**				**
Reduce territoriality	**	?	?	?	?	?	
Drink water		**	*		**	**	?
Group huddling	?	*		**	?	?	?
Reproduction							
Forego reproduction	**		?	?	?	?	
Rapid reproduction	?	?	**	*	?	?	**

* Moderate; ** well-developed; ? not known; blank, absent or poorly-developed; NA, not applicable for ectotherms.

Physiological ecology
Chuckwalla lizards

Chuckwallas are diurnal, sun-basking lizards which have a remarkably large number of adaptations that aid survival in the Mojave Desert (Table 1). These animals maintain

relatively constant plasma electrolyte concentrations and proportional body fluid compartments throughout the year, despite wide swings in the availability of water. They have very low rates of evaporative water loss, and they can produce quite dry feces and urine (Nagy, 1972). Nasal salt glands combine with precipitation of salts with urates in urine to eliminate the substantial dietary salt loads with little loss of water.

In spring, chuckwallas emerged from winter hibernation underground, and began eating the rapidly-growing annual herbs available then. This diet contained abundant digestible energy and nitrogen (Nagy & Shoemaker, 1975), but it also had high levels of potassium and much more water than the lizards needed to maintain balance. Chuckwallas excreted the excess water as copious urine, rather than storing it somewhere in the body. They were active about 8 hours each day (Nagy, 1973).

When annual plants began drying up in late spring and early summer, chuckwallas continued feeding and were able to maintain energy balance, but they began losing weight. They stopped eating annual plants and consumed only perennial plant foods, which were still moist at that time. This diet contained much less water, higher electrolyte concentrations and lower amounts of digestible nitrogen than their early spring diet, but chuckwallas were able to maintain relatively constant plasma electrolyte concentrations and body fluid proportions by using their physiological capabilities for conserving water and eliminating excess salts.

During the summer drought, chuckwallas responded to the lack of moist, green vegetation by not eating. They estivated in rock crevices all summer, emerging for only an hour or so near sunset every third day on average. While aphagic and estivating, chuckwallas lost water and body mass slowly, but they regulated plasma electrolyte concentrations and relative body fluid volumes, apparently by intermittent activity of their nasal salt glands to eliminate excess ions. When rainwater from rare summer thundershowers became available, chuckwallas did not emerge from crevices to drink. It is suspected that drinking water in summer may be detrimental to their carefully-maintained plasma electrolyte concentrations. Estivation behavior reduced energy metabolism by about 70%, and water losses declined by about 90% compared to spring. As a result of this behavior, body dry matter and body water declined in proportion to each other, so that body compartments remained in approximate balance with each other, on a percentage of live mass basis. Chuckwallas continued estivating until mid-autumn, when they entered underground burrows to hibernate overwinter. Rates of water flux and body mass loss during hibernation were low but measurable (Nagy, 1972).

During the year that chuckwallas were studied, rainfall was below normal. These lizards were able to feed for only 70 days during spring (19% of the year). They entered winter burrows weighing only 63% of their weight at emergence the previous spring, and they lost an additional 9% of spring body mass while hibernating. Lizards showed no evidence of gonadal development at any time during the year, even in mid-spring when they were gaining weight rapidly. These lizards are apparently able to forego reproduction in poor years. Moreover, there was much overlap in home ranges of individual lizards throughout their activity season, especially in preferred feeding areas, indicating that they can also abandon costly social behavior in years when succulent food resources are scarce. In short, chuckwallas make use of several physiological, behavioral, morphological and natural history adaptations to maintain relatively good homeostasis throughout a year.

Desert tortoises

These diurnal, herbivorous reptiles, which live in the Mojave Desert, also possess a variety of adaptations (Table 1), but in contrast with chuckwallas, tortoises have body compositions and plasma electrolyte concentrations that vary widely during the year. Tortoises do not possess functional salt glands, but they have low rates of evaporative water loss and can store water and electrolytes in their bodies. The main features of the physiological ecology of desert tortoises are (1) their ability to tolerate large imbalances in their water,

energy and salt budgets on a daily basis while achieving balance on a yearly basis, and (2) their behavioral properties of spending relatively little time active above ground, and their remarkable skills at obtaining rainwater for drinking (Nagy & Medica, 1986).

Tortoises began emerging from winter hibernation burrows in early spring, but they spent only about 3 hours every fourth day abroad, feeding on succulent annual plants. They did not excrete the excess water and potassium present in that diet, but stored them as urine in their urinary bladders. As a result, their body masses increased, and urine osmotic concentrations increased until they matched plasma osmotic concentrations, then both increased. The spring diet was not only osmotically stressful, it apparently did not provide adequate supplies of digestible energy, and the dry matter content of tortoises declined somewhat due to metabolism of body substance.

In late spring and early summer, annual plants dehydrated, and tortoises switched to eating grasses. This relatively dry diet provided inadequate water, but energy intake exceeded metabolic needs. Thus, tortoises lost body mass due to water imbalance, but the dry matter content of their bodies increased. Osmotic concentrations in plasma and bladder urine remained high (320–360 mosM). As this drought period progressed and ambient temperatures climbed, tortoises spent progressively more time estivating in burrows, emerging for only 1 hour every sixth day on average.

This estivation ended in midsummer, when tortoises emerged just before, during, and shortly after thundershowers, and drank large amounts of rainwater that pooled in natural or tortoise-constructed depressions in the soil (Medica *et al.*, 1980). Tortoises voided their urinary bladders, their plasma osmotic concentrations dropped to 290–300 mosM, dilute urine accumulated in their bladders, and they averaged a 13% gain in body mass. After the rain, tortoises fed every 2–3 days on dry grasses and forbs, and accumulated much surplus energy. However, they were in negative water balance, lost body mass, and their bladder urine became quite concentrated again. As summer ended, more rain provided drinking water, and tortoises again 'flushed' themselves and accumulated dilute urine. They continued feeding on dry grasses until switching to newly-germinated annual plants.

As ambient temperatures declined during autumn, activity declined, but tortoises continued feeding on succulent annual plants. As in spring, tortoises were not assimilating quite enough energy to meet metabolic needs, but they accumulated excess dietary water and salts, and body mass, and plasma and urine osmotic concentrations increased. Tortoises entered hibernation in mid-autumn, and had very low rates of energy metabolism, water loss and weight loss through winter. Tortoises emerged the following spring with about the same body condition as they had a year earlier, but body masses were about 9% higher. By tolerating energy, water and salt imbalances on a daily basis, tortoises were able to exploit the periodically-available resources of the desert, and achieve balance and growth on an annual basis. This flexibility may account in part for the observation that desert tortoises were able to lay eggs each year, even during a drought year (Turner *et al.*, 1986).

Jackrabbits

Even though jackrabbits are also herbivores and they live in the Mojave Desert, their physiological ecology is quite different from those of chuckwallas and desert tortoises. Jackrabbits, by comparison, have relatively modest specializations for maintaining water, salt and energy balance, and most individuals apparently do not survive the dry seasons during typical years. The relatively few individuals that live in 'oases' where green vegetation is available year-round do survive, and apparently repopulate the desert each spring via their great reproductive capabilities.

In spring, jackrabbits maintained water, salt and energy balance while consuming a variety of succulent annual plants (Nagy *et al.*, 1976; Shoemaker *et al.*, 1976). They excreted excess dietary water and salts as urine. As the warm season drought progressed

into summer, jackrabbits reduced their energy and water requirements by being active at night and remaining inactive in shade during the hot daylight hours (Costa *et al.*, 1976), by tolerating modest hyperthermia and hypothermia, and by having moderately concentrated urine, moderately low evaporative water losses, and quite dry feces (38% H₂O). Even though jackrabbits selected relatively moist perennial vegetation to eat in late summer and autumn, they were unable to obtain adequate water to balance their water losses. In late autumn, before winter rains began, jackrabbits consumed dry annual plant remains, and bark and small stems of woody shrubs, apparently the only non-poisonous, moisture-containing plant matter remaining in the habitat at that time. This diet was not only inadequate regarding water, it also did not provide sufficient digestible energy and nitrogen. Thus, autumn and winter (before rains began) was the most stressful time of year for jackrabbits.

Those jackrabbits having home ranges that did not include a year-round source of green vegetation (either natural springs, seeps or oases, or man-made green areas) presumably perished before winter rains occurred. This suggestion is consistent with many reports (summarized by Nagy *et al.*, 1976) of mass-mortality observed in desert jackrabbit populations during late summer and autumn. Apparently, jackrabbits do not persist in deserts by relying primarily on physiological, morphological or behavioral adaptations which facilitate maintenance of water and energy balance, but instead by means of opportunistic exploitation of oases, coupled with a great reproductive output when conditions are favorable.

Antelope ground squirrels

These diurnal, omnivorous rodents also live in the Mojave Desert. They have good physiological adaptations for conserving water and energy, including low evaporative water losses, fairly concentrated urine, very dry feces, excellent capabilities for hyperthermia and moderate hypothermia (Karasov, 1981, 1982, 1983a; Chappel & Bartholomew, 1981). Perhaps more striking, however, are their behavioral adaptations, such as minimizing the time they spend abroad exposed to the desert climate, huddling together in winter (which reduces energy expenditure about 40%) and careful selection of diet items to meet nutrient requirements (Karasov, 1983b, 1985).

In spring, ground squirrels ate mostly succulent vegetation, along with some seeds, arthropods and carrion. This diet provided ample nutrients, and the excess water was voided as dilute urine. As annual plants died and perennial plants dehydrated in summer and fall, ground squirrels consumed more arthropods and seeds, and selected perennial plants over annual plants. Field water fluxes dropped by half, as animals conserved water more effectively and maintained water balance. Ground squirrels apparently did not drink rainwater when it was available in summer, but they benefited from it none the less by consuming annual plants that germinated following rains that fell during one of the two study years (Karasov, 1983a).

Vegetation had the lowest nutritional quality in autumn and early winter before the winter rains. At that time ground squirrels consumed mostly the leaves and seeds of tumbleweeds (*Salsola iberica*), an annual plant which has a deep tap root and which remains green much later in the year than do other plants. However, even this food was too dry to provide adequate water, and ground squirrels achieved water balance by consuming arthropods. After winter rains, annuals again became available and were consumed. Ground squirrels did not hibernate, but remained active throughout winter and huddled together in burrows (which conserved energy).

Thus, Antelope ground squirrels, like jackrabbits, faced the challenge of progressively drier and lower-quality plant food from early summer to early winter. Unlike jackrabbits, ground squirrels maintained water and energy balance throughout this period, primarily by selecting arthropods and seeds for consumption.

Chukar Partridges

These phasianid, ground-dwelling birds have a wide, generally mesic-habitat distribution, but they inhabit the Negev Desert at the margin of their range. Chukars are primarily granivorous, but they include substantial, and seasonally-variable, amounts of vegetation and arthropods in their diet. They require drinking water to maintain water balance, especially during the warm seasons, and are usually found near oases (Alkon *et al.*, 1982, 1985; Degen *et al.*, 1983, 1984). Their use of drinking water, along with their modest physiological and behavioral adaptations to deserts, allows them to maintain water and energy balance through most of the year. The most stressful season appears to be the winter period following the rains, when energy may become a limiting resource.

In spring, the diet of Chukars was about 45% vegetation, which provided enough water to make Chukars relatively independent of drinking water. During the hot summer, seeds made up 80% of the diet, vegetation accounted for only 18%, and Chukars had to supplement their dietary water intake by drinking. As the drought continued into early winter, the diet changed to 58% seeds, 35% vegetation, and arthropods increased from 2 to 7% of the diet, but Chukars still obtained more than 25% of their water supply by drinking. Chukars were able to maintain or increase body mass from spring through early winter.

In late winter, after rains fell and seeds germinated, Chukars were not able to maintain energy balance, and they metabolized their fat reserves (Kam *et al.*, 1987). The cool, wet conditions apparently imposed energy demands on the birds that they were not able to meet by food alone. They were consuming more than 90% succulent young vegetation, and less than 8% energy-rich seeds, apparently because most seeds had already germinated. This diet contained much water (so Chukars did not have to drink), but it had little digestible energy, much like the situation for desert tortoises in spring (see above). It may be that seed-eating birds, which have muscular crops that pulverize ingested seeds, are unable to process low-energy foods rapidly enough to meet seasonally-high energy demands. Chukars remained in the study area through winter, surviving by relying on fat deposits to make up dietary energy deficits until weather conditions improved. This was not the case for Sand Partridges, which lived in the same habitat.

Sand Partridges

These diurnal, phasianid birds live in the Negev Desert and rely heavily on permanent sources of drinking water during the dry seasons. They were thought to be totally granivorous, but recent diet studies show that they also consume much vegetation (Alkon *et al.*, 1982, 1985; Degen *et al.*, 1983, 1984; Kam *et al.*, 1987). Sand Partridges apparently do not eat arthropods. These birds are weak fliers, they do not burrow, and thus spend most of their time on the soil surface. The most difficult season for Sand Partridges appears to be winter following the rains, when available foods do not provide adequate energy.

In spring, the diet of Sand Partridges was about two-thirds vegetation and one-third seeds. This diet provided adequate nutrients and water, and the birds did not drink from oases. As the drought progressed through summer and fall into early winter before the winter rains, Sand Partridges consumed relatively more seeds (up to 85% of the diet), and drank water to achieve water balance. After winter rains, Sand Partridges apparently left the Negev Desert and moved to the hotter, drier Judean desert until spring, when they returned to the Negev. Evidence from Chukar Partridges (above) suggests that a relative lack of an energy-dense food source (seeds, most of which germinated after rains), coupled with cool, wet conditions, imposed energy demands upon Sand Partridges that were greater than could be supplied by the available succulent vegetation, which contained much less digestible energy per unit fresh mass.

Side-blotched lizards

The only carnivorous desert animal for which detailed annual field data are available are side-blotched lizards, which are small (3 g), diurnal insectivores. These lizards use burrows as retreats at night and during unfavorable weather, but they are active intermittently throughout the year in the Mojave Desert. Reproductive output can increase dramatically in favorable years, when rainfall is high (Turner *et al.*, 1974, 1976).

Primarily by virtue of their diet, these lizards maintained water balance throughout the year, and they experienced slightly negative energy balance only during midwinter, when low ambient temperatures restricted feeding (Nagy, 1983; Nagy & P. A. Medica, unpublished results). Although newly-growing annual plants were important diet items in spring, these lizards consumed only arthropods most of the year. Because living animals (arthropods) are water- and energy-rich foods, side-blotched lizards did not face the problem of seasonally low food quality experienced by plant-eating desert animals. Instead, these lizards may have faced food *quantity* problems in some seasons. In spring, larvae of moths and butterflies, grasshoppers, spiders, hemipterans and flies were important dietary items. However, these ephemeral arthropods essentially disappeared after midsummer. Then, side-blotched lizards consumed termites, beetles and ants, which, because of their own adaptation to deserts, are able to remain active in hot, dry seasons.

These lizards have rather ordinary physiological and behavioral capabilities for maintaining water and energy balance, even when compared with nondesert diurnal lizards of similar size. These capabilities include low evaporation, moderately dry feces and urine, functional nasal salt glands, use of burrows (which reduces water and energy needs), and large body fat stores in some seasons (Table 1). Side-blotched lizards apparently were abroad and active whenever microenvironmental conditions permitted them to attain and maintain body temperatures appropriate for activity. Their key to desert survival seems to be diet selection. They prey upon other animals that are adapted to deserts in their own rights. Thus, side-blotched lizards may be viewed as making use of the adaptations of other desert animals. Most desert carnivores probably do this, and it would appear to be an automatic advantage conferred on carnivores simply because of their position in the food web.

Seasonal survival patterns

It seems clear that each of these seven species uses rather different mechanisms to survive in deserts. Within broad trophic levels, the problems and the general nature of the solutions are similar: herbivores face low-quality food during summer, autumn and early winter, and they respond by not eating or by eating some and suffering the consequences (imbalance or death); omnivores opportunistically take advantage of whatever foods are available, but may nevertheless face stressful periods; and carnivores face a food quantity rather than a food quality problem which they solve by selecting prey items (Fig. 1). Despite these general patterns, the closer we look at individual species, the more differences there seem to be. For example, among plant-eating reptiles, chuckwallas function so as to maintain homeostasis within relatively narrow limits through the year, whereas desert tortoises tolerate wide swings in body condition as the seasons progress. Jackrabbits appear to have few well-developed adaptations that aid them in maintaining water and energy balance in deserts, but they persist on account of their ability to reproduce rapidly and repopulate deserts from a few oases that serve as drought havens.

Adaptations to desert habitats may bring constraints along with them. Sand Partridges, for example, are able to tolerate high temperatures that exist at ground level in summer, but cool, wet conditions in winter, coupled with an apparent lack of energy-rich foods, seemed to impose sufficient stress on these birds that they migrated to warmer areas. Also,

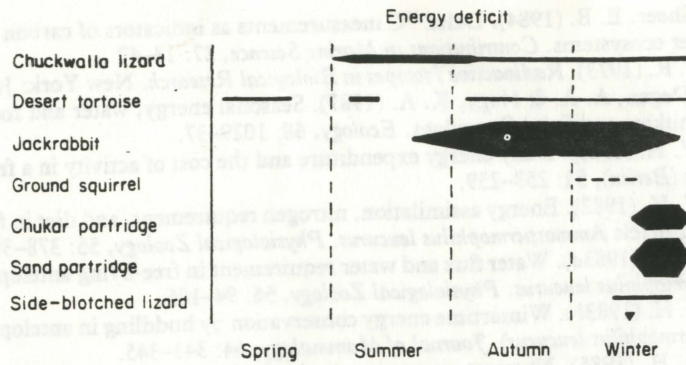


Figure 1. Comparison of annual periods of nutrient stress, indicated as energy deficit due to food energy intake being inadequate to meet energy metabolism, for seven species of vertebrates living in winter-rainfall deserts.

the remarkable ability of chuckwallas to regulate the osmotic and fluid volume status of their bodies may prevent them from using rainwater in summer, whereas tortoises which are more flexible regarding fluid and salt homeostasis, do drink and store rainwater and can continue to feed in summer as a result.

Each species of desert animal that has been studied in detail in the field has revealed a unique suite of mechanisms it uses to survive through a year. If this trend is representative, then a rich diversity of desert adaptations awaits discovery. It is possible, even likely, that a given species does things differently from year to year, in response to the highly variable climates that are characteristic of many deserts. The seven species discussed above were studied for only 1–2 years. Moreover, all seven species live in winter-rainfall deserts. Little is known about annual survival patterns of animals native to summer-rainfall deserts, such as the Chihuahuan Desert in Mexico and the Kalahari Desert in southern Africa, or the deserts with unpredictable, aseasonal rain, such as the Atacama Desert in Chile and the great interior deserts in Australia.

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