Frogs and Toads in Deserts

Amphibians seem unlikely desert denizens. But those living in dry climes reveal a diverse and unusual array of adaptations to life at the extremes

by Lon L. McClanahan, Rodolfo Ruibal and Vaughan H. Shoemaker

With their moist skin and aquatic tendencies, frogs and toads seem best suited to life in or near bodies of water. Yet these creatures are found in arid regions throughout the world—from the Colorado Desert in California to African savannas. To survive in such climates, they have developed behavioral and physiological mechanisms that allow them to conserve water and remain cool.

The range of adaptations that we and other researchers have observed challenges some of the classical views of anuran, or frog and toad, physiology. Most of our previous knowledge was based on temperate species. The study of desert-dwelling amphibians has offered insights into the remarkable diversity of these animals.

Some 300 million years ago amphibians were the first vertebrates to invade the land, and they maintain a strong connection to fresh water. Modern amphibians include salamanders, caecilians—legless amphibians that resemble worms—and anurans. Contrary to most people's perception, no biological distinction separates frogs and toads: terrestrial anurans with warty skins are usually called toads; aquatic forms with smooth skins are called frogs. Most amphibians lay their eggs in water and have larvae that lead a fishlike existence until they undergo metamorphosis. Once equipped with legs and lungs, they spend at least some time on land.

Despite the ability to survive on terra firma, most amphibians inhabit sites near fresh water or areas of elevated humidity and rainfall. Relatively few live in arid regions. This geographic distribution reflects the physiology of amphibians: they are generally ill suited to face the rigors of the desert.

Other terrestrial vertebrates, including reptiles, birds and mammals, have an integument, or skin, that can protect them against desiccation. The outer part, known as the stratum corneum, is composed of multiple layers of flattened, dead epidermal cells. This skin deters water loss. Unlike these other vertebrates, amphibians typically have a stratum corneum consisting only of a single-cell layer. This very permeable skin offers some benefits. Amphibians do not drink but absorb water across the skin from moist surfaces, such as wet rocks or leaves, and soil as well as from pools. Oxygen and carbon dioxide pass readily through the skin; for example, lungless salamanders rely on the integument for gas exchange.

At the same time that it is ideally suited to absorb water, the thin amphibian skin is a perfect conduit for evaporation. Under moderate conditions of temperature and humidity, most amphibians cannot survive for more than a day in circulating air because they quickly dehydrate. Even anurans, which can tolerate much larger water losses than can other vertebrates, are jeopardized in this situation.

Amphibians also differ from other vertebrates in the way they excrete wastes. The kidneys of desert animals are challenged to conserve water while eliminating the nitrogen waste produced during the metabolism of protein and other nitrogen-containing compounds. Birds and reptiles have solved this problem by synthesizing uric acid, a poorly soluble, nitrogen-rich compound. This waste can be excreted as a solid precipitate, and little water is lost. Mammals incorporate their

LON L. McCLANAHAN, RODOLFO RUIBAL and VAUGHAN H. SHOEMAKER have spent more than 20 years studying desert frogs and toads. Their association began in 1965, when McClanahan was a graduate student working with Ruibal at the University of California, Riverside, and Shoemaker arrived there as an assistant professor. The three of them formed a lasting friendship that led to research ventures in North and South American deserts. In particular, they discovered bizarre amphibian adaptations in the unique habitat of the Gran Chaco in Argentina and Paraguay. Ruibal and Shoemaker are professors of biology at Riverside; McClanahan is professor of biology at the California State University at Fullerton and director of the university's Ocean Studies Institute.

TREE FROG *Phyllomedusa sauvagei* is one of several species of frog adapted to arid regions. This South American anuran can survive in hot, dry environments because it tolerates high body temperatures. It also conserves water by losing little liquid through its skin or from its excretory system.

waste nitrogen into urea, a water-soluble molecule. They conserve precious water by creating urine that has a high concentration of dissolved materials, primarily urea and salts. This ability is particularly well developed in desert rodents. The kangaroo rat, for instance, produces urine that is 14 times as concentrated as blood; Australian desert mice achieve ratios of 20 or more.

Like mammals, adult anurans usually produce urea, but in contrast to mammals, they cannot make urine that is more concentrated than blood. They therefore require a great deal of water to eliminate their waste. Most amphibians are also less tolerant of high body temperatures than are other terrestrial vertebrates. Birds, mammals and desert lizards can maintain body temperatures of about 40 degrees Celsius. But many frogs and toads die at temperatures of 35 degrees C or less.

Terrestrial frogs and toads share some characteristics that help to offset the handicaps imposed by their permeable skin and inefficient kidneys. When water is unavailable, these animals stop producing urine and allow wastes to accumulate in the body fluids. Dehydration also results in beneficial changes in the skin and urinary bladder. Increased permeability of the bladder permits the animals to restore water lost by evaporation by reclaiming water stored as dilute urine. In addition, dehydrated frogs and toads absorb water through the skin much more readily than when they are hydrated. These responses are mediated by a posterior pituitary hormone called arginine vasotocin.

However useful in the short term, these protective measures do not permit anurans to survive without water for a long time in hot, dry environments. Thus, frogs and toads in these regions have evolved additional strategies. Perhaps the most straightforward adaptation to life in dry lands is to stay near what little water is available, and many species of amphibians do just that. Springs, seeps, canyons that drain higher ground as well as man-made impoundments are all permanent water sources where frogs can be found.

The frog *Hyla cadaverina,* or the California tree frog, found in the Colorado Desert, is one such oasis dweller. These frogs live near seeps and water holes. Although air temperatures often soar above 40 degrees C, the frogs' bodies do not exceed 30 degrees C, because they undergo evaporative cooling. *H. cadaverina* can store up to 25 percent of its body weight in the form of dilute urine. As it loses water through evaporation, water from urine is recycled back into the body. When these reserves are exhausted, the frogs return to the seep and take in more water.

The seeps also provide a place for mating and egg development. On summer days the frogs remain in clumped masses near water holes. The reasons for clustering in this fashion are not clear. We think huddling may decrease the amount of water lost by an individual. As evening approaches, the frogs slowly disperse and start to feed at the water's edge in preparation for night, when they chorus, mate and lay eggs in the pond. If rain forms other pools, the frogs will spread out and lay eggs in these waters as well.

The red-spotted toad, *Bufo punctatus,* uses the canyon waters of the Colorado Desert for spawning. But unlike *H. cadaverina,* these toads do not permanently reside in a moist environment. Using transmitters, we tracked toads that moved up to 100 meters

away from the water. Even in the middle of a summer day, we discovered toads burrowed in the coarse soil of rock crevices far from water. These crevices provide a shelter that is shared with other members of the same species: at one site we found eight individuals in the same cranny.

Because *B. punctatus* is unable to tolerate temperatures higher than 35 degrees C, we presumed that the toads seek microhabitats that remain relatively cool during the day. Studies using implanted location and temperature sensors confirmed this theory. We tracked one toad from September, late in the active season, until December, one of the colder months. At night dur-

Anuran Adaptations in Arid Regions

COLORADO DESERT

Hyla cadaverina
(top left)
This frog lives near permanent water supplies in the desert. It can store up to 25 percent of its body weight as dilute urine. If it loses water through its skin, the frog can reabsorb water from the bladder.

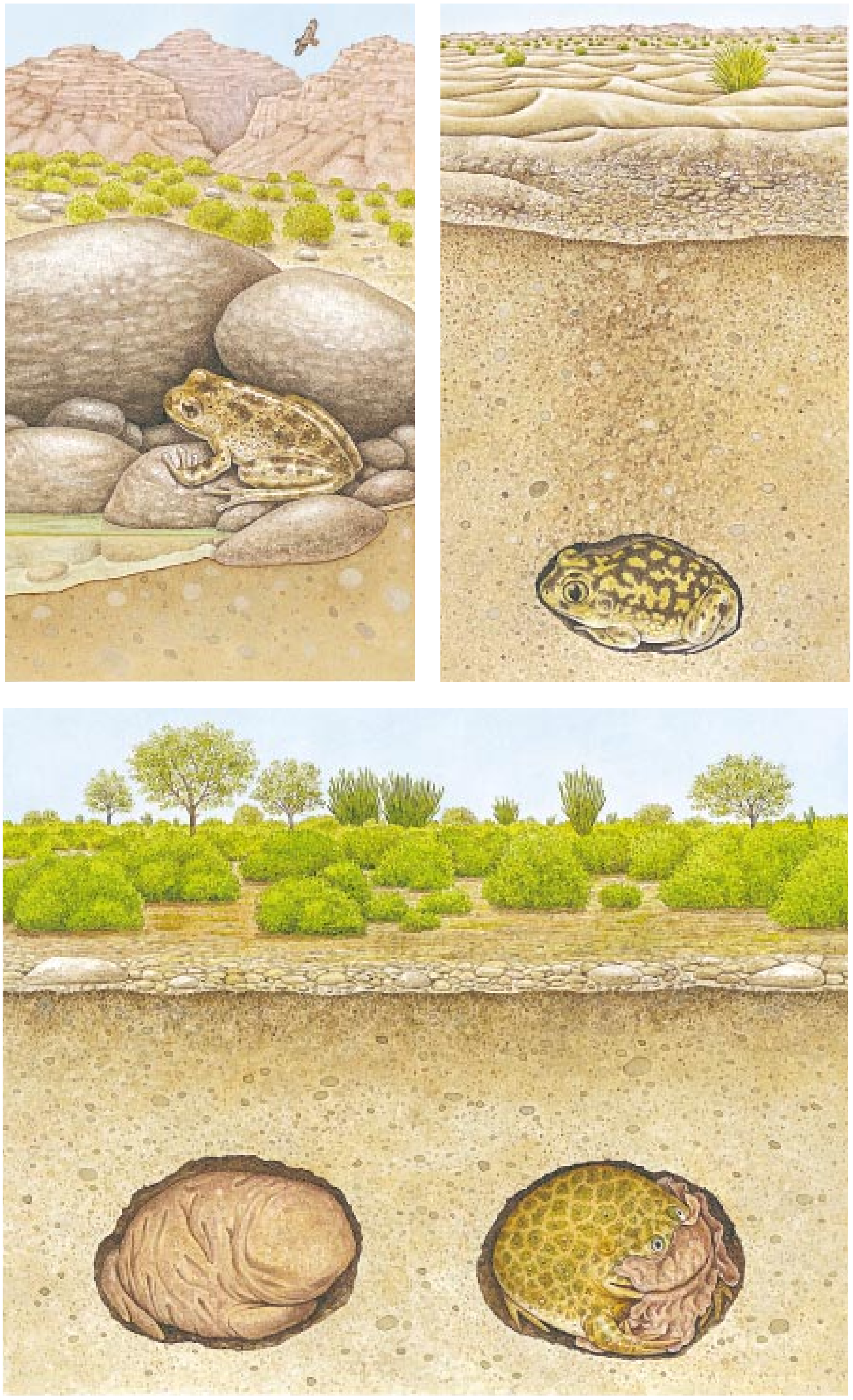
Scaphiopus couchi
(top center)
This species of spadefoot toad inhabits areas of the desert where there are no year-round water sources. To survive the dry season, the toad buries itself as deep as one meter underground. Some spadefoots have survived two-year droughts in this manner.

Bufo punctatus
(top right)
This toad can travel 100 meters from water sources, looking for food. To stay cool, it finds rock crevices and, like *H. cadaverina,* recycles water from urine. The toad can tolerate losing 40 percent of its body water (in contrast, camels can survive a 20 percent depletion).

GRAN CHACO REGION

Lepidobatrachus laevis
(bottom left)
This toad survives dry periods by burrowing into mud and becoming entombed. It then constructs a multilayered cocoon (*left side of panel*) to resist water loss. At the beginning of the rainy season, the toad pulls the cocoon over its head and eats it (*right side of panel*). Afterward *L. laevis* emerges.

Phyllomedusa sauvagei
(bottom right)
This tree frog coats itself with a waxy substance to prevent water loss. It also excretes uric acid to conserve water. *P. sauvagei* is the only anuran known to drink water—most absorb it through their skin. It does so by letting drops roll into its nearly closed mouth.



ing the warm season, it traveled 85 meters from its burrow to a small stream; early in the morning the toad returned to the same burrow.

The strategy is clearly successful. During the toad's active months, daytime air temperatures routinely exceeded the critical limits for the toad, but its body temperature never rose above 31 degrees C. Reduced temperatures in the burrow as well as evaporation controlled the toad's body temperature. Habitat selection also proved vital when the toad became inactive in winter, protecting it from cold nightly temperatures. In December, when air temperatures ranged from 12 degrees C at sunset to four degrees C at sunrise, the toad's body temperature inside the burrow remained constant at 25 degrees C.

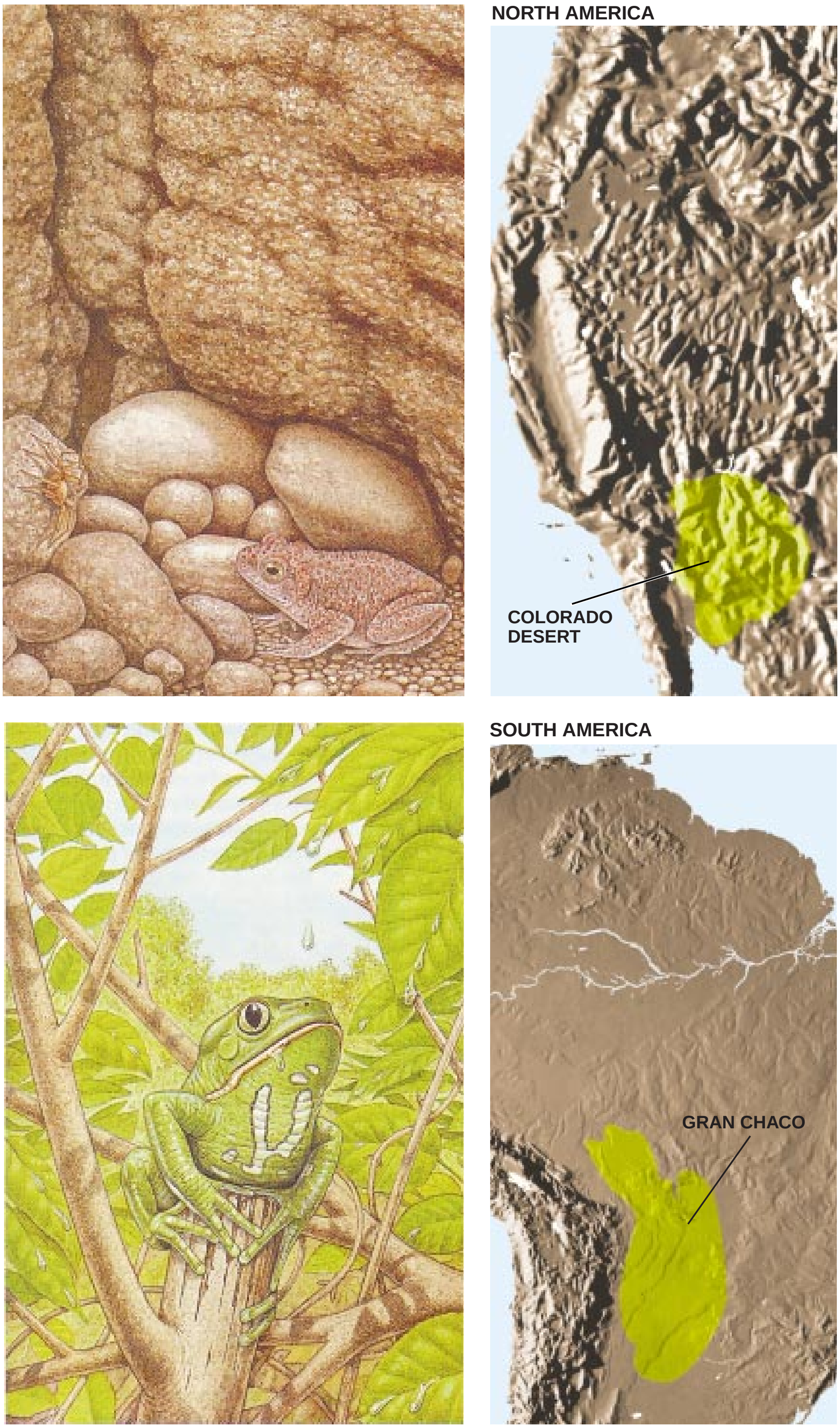
Not only does *B. punctatus* choose protective habitats, it possesses a characteristic that allows it to abandon its water source and forage for insects during hot summer nights. The toads can store 40 percent of their body weight as dilute urine. If all the bladder reserves are used, the toads have another safety feature: they can tolerate the loss of up to 40 percent of their body water. Humans can survive only a 10 percent loss of their body water; camels, 20 percent.

Most areas of the desert lack permanent water sources. Amphibians that live in such regions do not retreat to rocky crevices; they burrow underground. The soil protects anurans from the extreme surface heat during the dry season. They obtain water through the soil, and as the earth dries, they conserve water because little is lost to evaporation.

We first studied the ecology of burrowing toads in southeastern Arizona. Three species of *Scaphiopus,* or spadefoot toads, are abundant in this area and can easily be found after the summer rains bring them out of the burrow. Although some toads emerge during light rains, the majority come out during the evening of the first heavy downpour, when temporary ponds form. We wondered what cues might trigger this exodus. We determined that gently and silently moistening the soil by pouring water on it did not elicit a response, whereas sprinkling the soil to imitate rain caused the animals to surface. The toads came out even when the ground was kept dry with plastic. Sound alone is a sufficient cue.

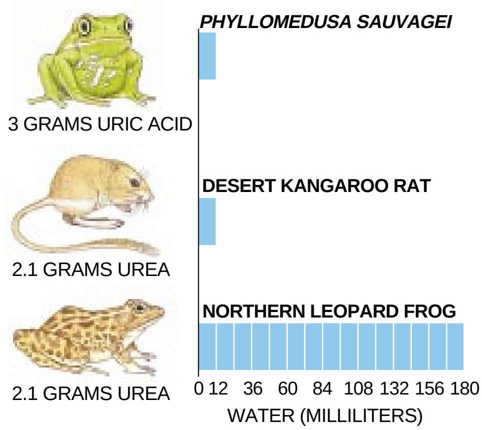
After they have left the burrow, adults make their way to the ponds to breed. Toads captured on the way often have a stomach full of termites that have simultaneously emerged from their underground nests. Spadefoots have a prodigious appetite and can consume 55 percent of their body weight in a single night. One meal of lipid-rich termites can provide enough energy to maintain a toad for more than a year; it may even be sufficient to allow a female to produce eggs.

Once in the water, the toads usually stay about 24 hours, just long enough to mate and lay eggs. They then leave and sometimes travel miles to take up



Comparison of Nitrogen Excretion*

Most amphibians, such as the northern leopard frog, excrete nitrogen as urea in solution, using ample water. Desert-dwelling mammals use less water to excrete the same amount of urea. Desert frogs, such as *Phyllomedusa sauvagei*, resemble mammals in that they use little water; they differ in that they excrete nitrogen waste as precipitated uric acid.



*per gram of nitrogen

residence in shallow burrows. On windless nights they forage on the still damp desert floor. The toads return to the burrow after feeding, reburying themselves in the friable soil. By late summer they disappear and are not seen until they unearth themselves the next summer. In parts of the Colorado Desert, one of the spadefoot toads, *Scaphiopus couchi,* was found to survive for nearly two years without rain. Fat reserves are sufficient because the toad drastically lowers its metabolic rate during its retreat underground.

We considered whether spadefoot toads could regulate the composition of their body fluids while below ground. So before the rain came, we tried to locate toads by digging near the dried-out ponds where they breed; we even used a bulldozer to excavate a large area. We did not find any toads. Fortunately, one of the local ranchers informed us that he occasionally uncovered toads when digging holes for fence posts, some at the depth of nearly one meter. Moreover, the burrowed creatures were surprisingly far, at 100 meters, from the vanished pond.

Armed with this information, we were able to find some sites where buried toads could be excavated and studied. At a location in Arizona, we dug up toads at various times during the year. We took samples of plasma and urine and analyzed them for electrolytes, urea and total solute concentration. In addition, we measured the volume of urine in the bladder and the moisture content of the soil at the burrow site.

We discovered that from the time the toads burrowed in September until we unearthed them in March the solute concentration in plasma and urine was typical of fully hydrated anurans. Furthermore, in March most individuals had retained a lot of dilute urine in their bladders—an amount equivalent to between 25 and 50 percent of their body weight. The soil adjacent to the toads was also fairly moist, and the forces binding water to soil were sufficiently weak, so that water could move osmotically into the animal.

In late June, just before the first rains, the toads were still in excellent condition but contained high concentrations of urea in both plasma and urine. By then the soil had dried so much that water could not pass from soil to animal—unless there was enough buildup in the total solute concentration in the toads to overcome the increased forces binding water to the soil.

The accumulation of urea in the spadefoots' body fluids tilts this exquisite osmotic balance. In laboratory studies we have found that the toads can produce and store urea on demand. If they are placed in relatively dry soil, they make more urea than when they are in wetter soils. This same strategy of storing urea is used by frogs that can adapt to brackish water (there are no truly marine frogs). In this case, the accumulation of urea makes the body fluids more concentrated than those fluids surrounding the animal, causing water to enter the creature by osmosis. For the same reason, some marine fishes such as sharks and coelacanths also retain elevated concentrations of urea in the body fluids.

A bizarre burrowing toad from the family Ceratophryidae has an even more elaborate survival tactic than the spadefoot toad. Unlike spadefoots, these animals do not store high concentrations of urea in their body fluids; they depend on a cocoon to prevent water loss. These toads inhabit the Gran Chaco, a semiarid region that extends from north-central Argentina into Paraguay, where they live in temporary ponds that fill up during the summer rains. One of the creatures, *Lepidobatrachus laevis,* is voracious and pugnacious. It screams loudly and bites when threatened. The animal is known as kururú-chiní, or "the toad that shrieks," in Guaraní, the language of Paraguay.

Unlike spadefoot toads, the kururú-chiní remain in ponds during times of drought. As water evaporates, they burrow to a shallow depth and become entombed as the mud dries. The toads then start to produce a multilayered cocoon. The kururú-chiní is not alone in this practice. Various other burrowing species in Australia, Africa and Mexico are known to form cocoons—indeed, it seems cocoon formation evolved independently several times.

All anurans periodically shed the outermost cell layer of their skin after a replacement layer has been formed. During cocoon formation, however, the outermost layer of skin is not shed and stays in place as additional layers grow beneath. Indeed, the kururú-chiní forms a new layer every 24 hours until it is enclosed by a multilayered cocoon of flat cells with dried mucus between each layer. When plotted against time, evaporative water loss during cocoon formation shows a hyperbolic decline as each layer forms.

In the laboratory the kururú-chiní will construct a cocoon if it is deprived of water and placed in a quiet, dark place. Time-lapse filming shows that the toad moves only slightly as the cocoon thickens; after a few weeks, it remains motionless for days on end. But even when ensconced in its fully formed cocoon, the kururú-chiní retains its unnerving ability to shriek when disturbed. If the toad is gently moistened with water, it will awaken and start to shed the cocoon in one piece. The animal uses its legs to roll the cocoon up from the posterior part of the body, over its head. The kururú-chiní then promptly eats the entire wet casing.

Perhaps the most striking anuran adaptation to life in the desert was discovered serendipitously. In 1970 we received a surprising reprint from John P. Loveridge of the University of Zimbabwe (then Rhodesia). It described experiments showing that the gray tree frog, *Chiromantis xerampelina,* could survive for long periods in open, dry containers. The frog lost weight at a fraction of the rate of other frogs—rates similar to those of a lizard kept under identical conditions. Loveridge also noted that most of the dry mass of the frog's urine was uric acid.

His findings were heretical. All frogs and toads were thought to have water-permeable skins—with the exception of cocoon-forming burrowers—and to excrete nitrogen as urea. Loveridge's description suggested a frog with a

COLOR CHANGE permits *Chiromantis xerampelina* to endure direct sunlight. By abandoning its dark, protective coloring (*left*) and adopting white (*right*), the tree frog reflects the sun's rays. The frog also survives the heat by storing large volumes of water in its bladder and then using the reserve for evaporative cooling.

reptile's impermeable skin and a reptile's capacity to excrete uric acid.

At the time the paper appeared, we were beginning studies of amphibians in the Gran Chaco. We were impressed with the diversity of the amphibian fauna living in this region, which included a green arboreal frog, *Phyllomedusa sauvagei,* known locally as *rana verde.* Whereas most frogs living in arid regions must remain underground or near water, except during the rainy season, *Phyllomedusa* and *Chiromantis* can remain perched in trees, where they feed. *P. sauvagei* is active before the onset of summer rains in Paraguay, and *Chiromantis* can be found during the dry season in Zimbabwe. Because of Loveridge's work, we made crude measurements of water loss in *P. sauvagei* in the laboratory, but we observed nothing unusual.

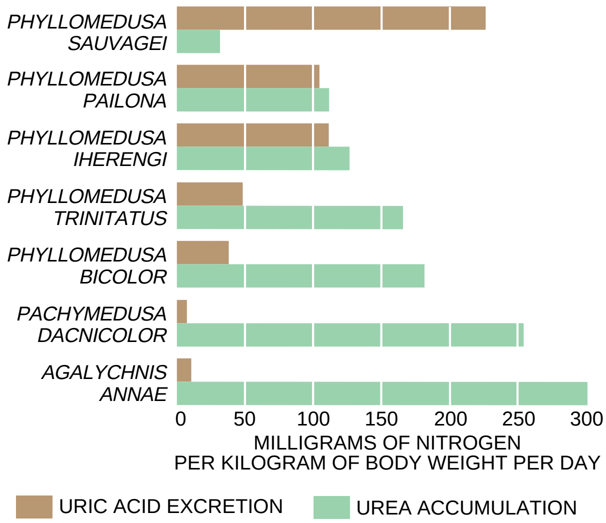
A few weeks later one frog voided a large blob of semisolid urine while being handled. A quick trip to the spectrophotometer revealed that the major component was uric acid. Studies of nitrogen balance in *Phyllomedusa* and *Chiromantis* have amply confirmed the benefits of uric acid excretion. In both species, about 80 percent of the waste nitrogen is emitted as uric acid or urate salts. In addition, sodium and potassium precipitate along with uric acid, which further increases the excretory capacity of the kidneys. Thus, these frogs can feed while deprived of water for long periods. Across species, there appears to be a wide range in the ability to synthesize uric acid: from 230 milligrams per kilogram per day in *P. sauvagei* to only 40 milligrams per kilogram per day in *P. bicolor,* which inhabits tropical regions of Brazil.

The ability to make and excrete uric acid turned out to be only one aspect of the tree frog's adaptations. We remeasured the evaporative water loss in *Phyllomedusa*—with care and patience this time—and found that *Phyllomedusa,* like *Chiromantis,* could reduce its water loss to very low levels when it was allowed to perch and behave normally.

We had observed that the frog uses each foot in turn to wipe its entire body. After this ritual, *rana verde* looks as if it consisted of plastic. Water dripped onto the creature's skin beads up, as it does on a waxed surface. Histological studies revealed the presence in the skin of a novel form of gland, which was interspersed between the mucous glands and poison glands that are typically found in frogs. The glands are tiny and numerous, about 30 per square millimeter of skin; they stain intensely when treated with lipid-soluble dyes. It is now clear that the waterproofing process involves the synchronous dis-

WIPING ITS SKIN with each of its four legs, in turn, allows *Phyllomedusa sauvagei* to completely cover itself (*left*) with the waxy substance that it secretes to prevent water loss. Once coated, the frog appears to be made of plastic. The protective lipid is produced in tiny skin glands that are shown magnified 150 times and dyed red in this micrograph (*right*).

charge of these glands, immediately followed by wiping. The coating, a rather heterogeneous mixture of lipids, is primarily wax ester. Like *Phyllomedusa,* insects and plants use a variety of waxes to retard water loss. Curiously, *Chiromantis* does not have lipid glands. The mechanism by which it prevents evaporation remains obscure.



URIC ACID PRODUCTION varies greatly. Frogs in arid regions, such as *P. sauvagei,* convert 80 percent of their nitrogen waste into semisolid uric acid, reducing the urea in the blood and saving water. Tropical frogs, such as *P. bicolor,* convert 20 percent. (*Pachymedusa dacnicolor* and *Agalychnis annae* are closely related to *Phyllomedusa.*)

Phyllomedusa and *Chiromantis* are able to survive in very hot environments. They accomplish this remarkable feat by controlling their body temperature. Before the summer rains, the air may exceed 40 degrees C. Body temperatures of *P. sauvagei* were found to track air temperature, except during the hottest parts of the hottest days. At these times, the frogs remained about 40 degrees C—two to four degrees cooler than the air and three to five degrees cooler than a thermometer constructed to match the size, shape and absorptive characteristics of the frog.

The frogs achieve such thermoregulation by controlling evaporation rates. Laboratory work has shown that the frogs can match evaporative heat loss to increases in ambient heat over a wide range of temperatures, wind speeds and relative humidities. The mechanism appears to be analogous to sweating. Microscopic observation of the skin shows periodic discharge from many of the gland ducts that dot the skin. We presume but have not conclusively demonstrated that mucous glands are responsible. Pharmacological studies of *Chiromantis* indicate the glands are controlled by sympathetic nerves that stimulate beta-adrenergic receptors.

The regulation of body temperature requires the most water during the dry period, just before the summer rains. The frogs obviate this problem because they can tolerate high body temperatures. On most days, there is no need to evaporate water for thermoregulation; on very warm days, thermoregulation is required for a few hours.

Like other frogs, *Phyllomedusa* and *Chiromantis* can store large volumes of water in the bladder and use it to offset loss through evaporation. When bladder reserves are exhausted, the frogs allow body temperatures to reach even higher levels, thereby reducing the need for evaporative cooling. *Phyllomedusa* appears to remain shaded while perched in trees, at least for most of the day. *Chiromantis,* however, can be observed sitting in the full sun. *Chiromantis* minimizes the effects of solar radiation by undergoing a dramatic color change. It forsakes its gray or brown protective coloration and instead becomes white to reflect sunlight.

We wondered if *Phyllomedusa* could take advantage of the light rain that frequently precedes a heavy downpour. Because its skin is waterproofed, the animal cannot absorb moisture that way. Therefore, we performed experiments in which water was dripped on its head. Astonishingly, we observed *Phyllomedusa* lift its head to gulp drops of water. Experiments using water with dyes incapable of diffusing through the skin showed coloration in the esophagus, stomach and small intestine—the water had clearly been ingested, not absorbed. *Phyllomedusa* is the only anuran known to drink.

The study of amphibians in deserts and semiarid regions has revealed extensive and diverse specializations for terrestrial existence. The emerging picture of anuran physiology defies the stereotype based on earlier studies of temperate species. Similarly, amphibians in other habitats have other capabilities—such as tolerance to freezing—that were unknown until recently [see "Frozen and Alive," by Kenneth B. Storey and Janet M. Storey; SCIENTIFIC AMERICAN, December 1990]. Despite this diversity, or perhaps because of it, there is evidence of a worldwide reduction in some amphibian populations and the extinction of others. The decline is not restricted to any particular habitat.

Some instances are clearly the result of human intervention. Various places that were once home to spadefoot toads in southern California are now housing tracts. We have seen widespread destruction of the habitat of *Phyllomedusa* in the Gran Chaco, where trees are cut for fuel. Air and water contamination, the introduction of predatory fishes and even consumption of frog legs contribute as well. In some cases, humans encourage survival. The great abundance of spadefoot toads in southwestern Arizona is probably the result of cattle tanks constructed by ranchers to catch runoff from thunderstorms. Such facilities serve as breeding sites.

Yet populations of anurans have declined or disappeared in relatively undisturbed or protected places. Although a portion of such events may represent natural fluctuation, concern grows that amphibian decline may indicate subtle environmental deterioration on a global scale. The complex life cycles and reproductive specializations of amphibians may make them doubly susceptible. Desert-adapted species appear no better able to withstand the effects of human activity than are their counterparts in wet conditions. Even creatures that spend most of the year underground must find abundant food and suitable aquatic breeding sites when they emerge. To prevent further extinctions, it is imperative that we understand the panoply of and limits to the devices that frogs and toads use to thrive in all habitats.

FURTHER READING

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