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# Adaptations of Amphibia to Arid Environments

Novel physiological mechanisms not seen in fish aid frogs and toads to conserve water and live in deserts.

P. J. Bentley

Amphibia—frogs, toads, newts, and salamanders—have a worldwide distribution which excludes only the antarctic continent and most oceanic islands. There are three groups within the Amphibia, but they are unevenly distributed geographically and show some interesting differences with respect to the areas where they are principally found. Thus the Urodela (newts and salamanders) are nearly all found in the Northern Hemisphere and do not cross the equator, the little-known Apoda (coecilians) are confined to certain tropical equatorial regions in central Africa, South America, and southeast Asia, and the Anura (frogs and toads), which have the widest distribution, extend from arctic regions such as Alaska into the hot, dry deserts of Africa, Australia, and America.

People generally associate Amphibia with moist, cool areas, and it is at first somewhat surprising that they successfully occupy dry areas. Although certain physiological characteristics of Amphibia might be expected to result in hardship in such environments, small modifications of the basic physiological pattern result in an animal well able to survive in such hot, arid regions.

The principal problems of animals living in hot, arid areas arise from high environmental temperatures and

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rapid evaporative water loss, often accompanied by a limited water supply. One of the most striking features of the Amphibia is the presence of an integument which is quite permeable to water and cannot limit evaporative water loss. Furthermore the amphibian kidney, unlike that of birds and mammals, cannot form a hypertonic urine, so that Amphibia incur relatively greater urinary water losses. Amphibia produce eggs that are highly susceptible to evaporation and which usually must be deposited in pools of water to ensure embryonic and subsequent larval development.

The water metabolism of many amphibian species has been studied, and an impressive uniformity in their basic physiology is apparent. However, as will be shown, there are also differences which may contribute to the success of certain species in arid habitats.

## Temperature Tolerance

Amphibians are poikilotherms and compared to other terrestrial vertebrates have a low tolerance for high temperatures. Many anurans and urodeles die after a few hours' exposure to temperatures as low as 30°C, and they almost never survive at temperatures above 38°C (*1, 2*). However, like other poikilotherms, more particularly the fishes, many Amphibia can survive at higher temperatures after prior acclimation in moderately warm conditions. For instance, *Rana pipiens* previously kept at 5°C die after 1 hour of exposure to a temperature of 31°C, but after being kept for 1 to 3 weeks at 25°C this lethal maximum temperature is increased to 35.5°C (*1*). It seems likely that desert Amphibia may show physiological acclimatization with respect to their ability to tolerate high temperatures, but there is no definitive information on this. In addition, there may be inherent factors that can change this ability. For example, Schmid has shown (*2*) that the toad *Bufo cognatus* can withstand temperatures 2° to 3°C higher than *B. hemiophrys*, which occupies cooler habitats, can withstand. While the Anura and Urodela generally exhibit a poor tolerance for high temperatures, there is no information about the third group within the Amphibia, the Apoda, which are particularly interesting because they are confined to hot tropical regions.

## Evaporation and Water Uptake

Water is evaporated from the skin of Amphibia at a rate similar to that from a free water surface (*3*). This water loss is inversely related to the relative humidity, and, at a low humidity, can result in appreciable reduction of the body temperature below that of the environment (*4*). The rates of evaporative water loss suggest that the skin makes little difference and, as Adolph has shown (*4*), frogs without skin lose water at the same rate as intact animals. However, small differences in evaporative water loss among Amphibia have been found. For instance, Scala (*5*) and Rey (*3*) found that the European toad *Bufo bufo* lost water less rapidly than the frog *Rana esculenta* or the newt *Triturus cristatus*. Heller and I (*6*) have confirmed these results, but the differences are small; *Bufo bufo* loses water about 25 percent less rapidly than the other two species. In plethodont salamanders, Cohen has shown a difference of 35 percent in the rate of water loss of two species (*7*). On the other hand, Thorson (*8*) examined a number of American species of Anura and found only small differences in evaporation from their integuments, and such differences could not be related to any adaptation to the environments where the animals lived. Thus the significance of differences between rates of evaporation from the integuments of Amphibia is not clear, but assuredly all species so far examined still lose water very rapidly in this way.

Frogs in water do not drink but take up water by osmosis through their skin (*9*). There do not appear to be any reports of frogs drinking even after having lost considerable water by evaporation in air. Recently Schmidt-Nielsen and I (*10*) dehydrated some *Rana pipiens* so that they lost 25 percent of their body weight. When placed in water they regained this weight solely by water uptake through the skin. However, European frogs (*Rana*) dehydrated by being kept in hypertonic saline solutions drink the bathing media (*11*), and we have confirmed that the North American *Rana pipiens* will also do this (*10*). No amphibian species have been shown to drink under natural conditions, but it is possible that some may do so, especially in areas where the water supply is temporary or when an increased risk of predation during rehydration makes drinking advantageous.

The ability to absorb water through the skin may conceivably be an advantage. Amphibia can take water in this way from damp surfaces such as paper towels, moss, and soil (*4, 12*), and this ability may allow the animals far more latitude in their movements than if they were continually dependent on pools of water. Many species of Amphibia are in fact not generally found near free water except during the breeding season, and desert frogs may burrow down into damp soil around dried-up water holes and river beds.

The normal permeability of amphibian skin to water may differ from species to species (*13, 14*). In addition, it may increase in dehydrated animals, an effect which may be of considerable magnitude in many Anura and which appears to be at least partly mediated by hormones from the pituitary [see *15*; this hormonal effect has not yet been found in the Urodela (*16*)]. Thorson (*8*) attempted to correlate the speed of rehydration with the degree of aridity of the habitat occupied by a number of North American anuran species, but could find no indication that rehydration was more rapid in species occupying dry habitats than in those living in more moist areas. However, four species of an Australian anuran genus, *Neobatrachus*, exhibit differences in rates of rehydration consistent with an adaptation to the habitat (*17*). The different species of this genus extend successively from the wet coastal regions of southwest Australia into the arid interior. Species living in the arid regions of the interior rehydrated more rapidly than those from temperate coastal regions. Demonstration of such a difference has recently been repeated in members of this genus and also in other Australian frogs (*18*). In contrast, another Australian genus, *Heleioporus*, has five species that also live in areas of differing aridity, but no differences in the speed of rehydration of the various species was observed (*17*). *Heleioporus* are very efficient burrowers and since all species may thus be expected to experience a similar microenvironment, selective pressures conducive to increasing speed of rehydration may not operate.

Water makes up a higher proportion, about 80 percent, of the body weight of Amphibia (*19, 20*) than the 70 percent in most other terrestrial vertebrates. However, water content may vary between species; the tree frog *Hyla moorei*, for instance, has only 71 percent of its weight as water compared to 79 percent in *H. coerulea* (*21*).

About 25 percent of the body water in frogs and toads may be found in the lymph spaces, and this apparently represents a labile but isotonic supply of fluid influenced by the state of hydration of the animal (*22, 23*). Smith and Jackson (*22*) dehydrated *Rana pipiens* to 57 percent of their normal body weight and found that the water in the lymph spaces was reduced by 85 percent, contributing 45 percent of the total water lost. Vital organs such as the heart and brain maintained a nearly normal water content, and that of the muscles was reduced by 8 percent. Such a retention of water in the tissue cells relative to that in the lymph spaces could be of value for the survival of the animal and contribute to the remarkable ability of Amphibia to withstand dehydration.

As Amphibia lose great quantities of water, their body fluids become more concentrated. The body fluids of normally hydrated Amphibia have a concentration of 200 to 250 milliosmols, which is less than the concentration of 300 milliosmols found in most other terrestrial vertebrates. Most of this difference is accounted for by differences in the sodium concentration, which is about 110 milliequivalents per liter in amphibians and about 150 milliequivalents per liter in other terrestrial vertebrates. Whereas man has difficulty in surviving a concentration of sodium in the plasma of 170 milliequivalents per liter (about 330 milliosmols) frogs and toads can recover from body-fluid concentrations double that which is considered normal.

The kidneys of anurans stop forming urine when the animals are dehydrated (*9*), so that the recorded losses of 60 percent of the body water should result in large increases in concentration of the body fluids. Shoemaker (*24*) has measured body-fluid concentrations in dehydrated toads, and indeed they are directly related to the loss in body water (see also *11*). It has also been shown that the crab-eating frog *Rana cancrivora* can survive in salt solutions with a concentration of 850 milliosmols, maintaining their body fluid slightly hypertonic to such solutions (*25*). Both *Rana cancrivora* and *Bufo viridis* (*25, 26*) can survive concentrations of sodium in the plasma as high as 250 milliequivalents per liter (osmotically equivalent to about 480 milliosmols). Recently, experiments have been performed in which tissues of frogs and toads have been bathed in vitro in concentrated solutions of various solutes (*27, 28*). Muscles, for instance, can continue to contract when bathed in concentrated solutions, and there is evidence that muscles of species from desert areas are more resistant than those from wetter habitats (*28*). Thus the tissues of anuran Amphibia have a remarkable tolerance to change in their osmotic concentration, a fact which undoubtedly prolongs their survival in conditions where dehydration occurs.

Ability to withstand desiccation may vary considerably in different amphibians. Anurans and urodeles may withstand water losses equivalent to as much as 50 percent of their body weight, or 60 percent of their body water (*19, 29*). Survival during dehydration may vary considerably, depending on the speed at which dehydration proceeds, the temperature, and the general condition of the animal. It is therefore difficult to compare results carried out at different times in different laboratories. However, several uniform surveys have been performed, comparing the ability of anurans and urodeles from different habitats to survive various degrees of dehydration. Thorson and Svihla (*19*) and Schmid (*14*) found that North American anuran species from aquatic environments generally tolerate desiccation less well than those from drier areas. The aquatic frog *Rana grylio*, for instance, dies after losing water equivalent to only 30 percent of its body weight, whereas *Scaphiopus couchii*, which lives in deserts, loses 48 percent. Main and I found a similar correlation among four Australian species of *Hyla* (*21*). *Hyla moorei* from temperate areas dies after losing 30 percent of its body weight, whereas *H. coerulea* from the hotter north survives a 45-percent loss. A similar relationship to habitat has been observed in urodeles (*30*). Such a correlation is not invariably seen in all Amphibia from wet as compared to arid regions; frogs of the Australian genera *Heleioporus* (five species) and *Neobatrachus* (four species) all can withstand water losses equivalent to 40 to 45 percent of their body weight (*17*).

## Nitrogen Metabolism

The nature of the nitrogen excretion by Amphibia has been related to the habitat of the animals. Those living in fresh water, such as the South African clawed toad *Xenopus laevis*, excrete mainly ammonia, whereas more terrestrial species excrete urea (*30*). When *X. laevis* is dehydrated it changes to formation of urea, which is stored in the body to be excreted when the animal is returned to water (*31*), a situation also observed by Homer Smith in the estivating African lungfish *Protopterus aethiopicus* (*32*). In the toad *Scaphiopus couchii*, after prolonged periods of estivation in the Californian desert, McClanahan (*28*) has recorded osmotic concentrations as high as 600 milliosmols, the solute being largely urea. Vertebrate tissues withstand high concentrations of urea more readily than high concentrations of electrolytes, and Anura are no exception (*27, 28*). The crab-eating frog *Rana cancrivora*, living in concentrated saline solutions, may have concentrations of urea in the plasma as high as 480 millimoles (*25*). Amphibia living under arid conditions may utilize such a tolerance for urea in order to store catabolic nitrogen in a relatively nontoxic form, to be excreted at some subsequent time when more water is available.

The tetrapod urinary bladder has no anatomical homologue in the fishes and makes its first phyletic appearance in the Amphibia. This bladder is usually a large and very distensible structure. Townson in 1799 (*33*) described how the bladders of frogs and toads can store water which can subsequently be reabsorbed and utilized by the animal. More recently these observations have been confirmed, though not acknowledged (*23, 24, 34*). The bladders of different Amphibia vary somewhat in size, containing fluid equivalent to only 1 percent of the body weight in the aquatic toad *Xenopus* but as much as 50 percent of the body weight in the famous Australian desert species, the water-holding frog *Cyclorana platycephalus* (*6, 21*). Urodeles usually have smaller bladders than anurans, the largest we have observed being that of the European fire salamander, *Salamandra maculosa*, which holds fluid equivalent to about 35 percent of its body weight in the bladder (*35*). Such stores of water must be of considerable importance to desert frogs and toads, and even in more temperate areas they allow Amphibia greater freedom of movement away from water than would otherwise be possible.

## Hormonal Integration

Dehydrated anurans stop forming urine (*9*), most reabsorb water from their urinary bladder (*23, 24, 33*), and if placed in water they will take up fluid through the skin far more rapidly than they normally do. These responses are seen in most anurans with only one recorded exception, *Xenopus laevis*, which is aquatic and cannot alter the rate of uptake through its skin (*36*). The responses also occur when a hormone (vasotocin) from the amphibian neurohypophysis is injected, and it appears that hormones from this gland normally initiate such effects (see *15*). The neurohypophysis is a lobe of the pituitary gland which is present in all vertebrates and is the storage site of several hormones. Chemically these hormones are polypeptides consisting of a ring containing five amino acids and an attached side chain of three more. This is the basic structure of all vertebrate neurohypophysial hormones. The amino acid sequence was first worked out in the two mammalian hormones (*37*), oxytocin and vasopressin, the latter being principally concerned with the regulation of urine flow from the kidney. The Amphibia also possess two such hormones (*38*), and one of these affects water metabolism. Its structure is intermediate between that of the two mammalian hormones, consisting of the side chain of vasopressin and the ring of oxytocin, and thus it is called vasotocin.

Vasotocin is highly active in increasing water retention in many Amphibia, especially the Anura. The response of the urodeles is usually somewhat less than that of the anurans (*39*), probably because the urodeles do not increase the rate of water uptake through their skin (*14*). So far only one species of urodele, *Salamandra maculosa*, has been described which reabsorbs water from its bladder in response to the hormone. The kidney of *S. maculosa*, however, lacks an antidiuretic response (*35*). As in mammals, neurohypophysial hormones are probably also released in Amphibia during dehydration, for the store in the gland decreases under such conditions (*40*), and the plasma of dehydrated toads, when injected into other toads, causes them to retain water, an effect presumably due to vasotocin (*41*). It is interesting that the neurohypophysial hormones are found in fishes but do not seem to affect their water metabolism (*39*). The stores of neurohypophysial hormones increase dramatically in Amphibia as compared to the fishes, a situation which persists in other tetrapod vertebrates (see *42*). In all the tetrapods, starting with the Amphibia, these hormones bring about water retention and therefore may play an important role in the adoption of a terrestrial way of life.

## Behavior and Habitat

Amphibia may escape or moderate the effects of the climate in the region they occupy by selecting a microenvironment where conditions are more suitable. Many Australian anurans are confined to the vicinity of permanent water holes in the desert, whereas others can survive in the damp soil that remains after river courses and water holes have dried up. Some species are not confined to such obvious water sources and are found more widely in the desert (*43*). A few centimeters of soil may considerably moderate the desert conditions, and it has been observed that while the surface temperature of sand in the Sahara may be 60°C, 25 centimeters below the surface the temperature remains 32° to 33°C throughout the day (*44*). In addition, moisture from rains may remain trapped for years in sand at a depth of 20 to 30 centimeters, forming an unsaturated damp layer surrounded on either side by dry layers (*45*).

Desert frogs may avoid the heat and high rates of evaporation of the daylight hours by seeking refuge under litter or in cracks and crannies in rocks and soil. Thus the Australian tree frog *Hyla rubella* becomes cryptozoic when the water holes dry up, and some salamanders in Southern California lead a subterranean existence during the dry season (*46*). Other species have modified hind feet which allow them to burrow. *Heleioporus*, for instance, is a highly efficient burrower and has been found 80 centimeters below the surface (*17*). Frogs may seek refuge in burrows from which they may venture at regular intervals when conditions are cooler, or they may estivate for prolonged periods, emerging with the onset of rain. The Californian spadefoot toad *Scaphiopus couchii* estivates in burrows and on emergence is covered with a hard material, having the consistency of dried skin (*47*), which is functionally reminiscent of the "cocoon" seen in the estivating African lungfish. This "cocoon" may help limit evaporative water loss. Unfortunately, little information is available as to the conditions in such burrows, the survival rate, or the physiological condition of the animal after a prolonged sojourn in such a situation. In the desert areas of western Australia the number of frogs emerging after rain has been so vast as to interfere with the passage of trains, which are unable to maintain traction on rails made slippery by thousands of crushed frogs.

## Reproduction

The time for breeding in desert animals coincides with periods of rain (*48*). Most Amphibia lay eggs, and these eggs, which are highly susceptible to evaporative water loss, are usually deposited in water where the tadpoles grow to maturity. However, a few Amphibia, both anurans and urodeles, are viviparous, and others may deposit their eggs in protected places away from water where embryonic and even larval development may take place. Such arrangements would appear to have potential advantages for reproduction in arid areas, but there does not appear to be a correlation between mode of reproduction and habitat. Main, Littlejohn, and Lee (*43*), for instance, found that nearly all species living in the Australian desert laid eggs in water and that those that laid eggs away from water were principally confined to damp, temperate, forest areas. Desert frogs spawn when water is available, but if there is no rain they may not breed for several years (*43*). It is not yet clear whether dry conditions result in the suspension of the breeding cycle, with all its associated endocrine-controlled preparations, or merely inhibit oviposition. Water is not usually available for extended periods in deserts, and there is evidence that metamorphosis is accelerated in desert species (*43, 47*). It would be interesting to know whether this is an inherent ability or is related to environmental factors such as temperature or some stimulus resulting from the drying up of the pools of water.

## Summary

Undoubtedly the greatest physiological disadvantage which the Amphibia have to overcome in hot, dry habitats is their permeable skin, and the most valuable evolutionary novelty which they could invent to assist their survival there would be a more impermeable integument. This has not occurred in Amphibia, although it is seen in their phyletic offspring, the Reptilia. However, Amphibia do make the best of the situation and utilize the skin to collect water from damp surfaces and to assist rapid rehydration. Extra water can be stored in and subsequently reabsorbed from a large urinary bladder, a structure which has no homologue in their phyletic forebears, the fishes, but persists in other terrestrial tetrapods. Water transfer across the skin and bladder, as well as urine formation by the kidney, is controlled by hormones from the neurohypophysis, a mechanism which likewise is a phyletic innovation not present in the fishes. Amphibian tissues can continue to function in the presence of high osmotic concentrations of solutes, especially urea, so that the amounts of water loss or metabolic solute accumulation consistent with life are great, compared with those for other terrestrial tetrapods such as the mammals. Most important, the Amphibia have literally "used their heads" to find microenvironments where conditions are favorable for survival and reproduction. Much of this has indeed been said previously, for Townson in 1799 (*33*) described how frogs and toads "have power of absorbing the fluids necessary for their support . . . through the external skin . . . a large part of them appearing to be retained in the so called urinary bladder, though gradually thrown off again by the skin."

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