Reproductive Strategies of Frogs

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Reproductive Strategies of Frogs

The familiar progression from egg to tadpole is only one of many methods. Others include egg to froglet, egg brooding, and tadpoles in the mother's stomach

by William E. Duellman

In 1758 the German naturalist A. J. Rösel von Rosenhoft published what was then the definitive study of frog development. His magnum opus, with its detailed descriptions and meticulously executed drawings, provided the world with a close-up view of a frog's life cycle—from egg to tadpole to four-legged adult.

Yet Rosenhoft's work, which was based entirely on the common European frog, *Rana esculenta,* is now known to describe only one of many life-history strategies exhibited by frogs as a group. Among herpetologists (those who study frogs and their relatives), including myself, it is increasingly apparent that many species do not conform to the life cycle of the common European frog. Although some frogs adhere to its stereotypical mode of development (depositing thousands of small eggs that become free-swimming tadpoles), many more have evolved reproductive strategies that border on the improbable. Indeed, in reflecting on my 40 years as a field biologist, two thoughts come to mind. The first is frogs are never-ending sources of fascination; the second is they adhere to few conventions.

Frogs and toads (hereafter referred to collectively as frogs) are members of the amphibian order Anura, a term that means tailless in Greek and appropriately describes the adult form. Over the course of the 200 million years since anurans first appeared in the fossil record, they have differentiated into some 24 families and more than 3,800 species. The precise number of species is unknown because new frogs are discovered at a remarkable rate: several dozen are formally described every year. Another indicator of the group's success is the degree to which its members have dispersed across the planet. Today frogs inhabit all continents except Antarctica and have adapted to a breadth of environments, including deserts, forests and grasslands; some species even live at altitudes greater than 5,000 meters (19,685 feet) in the Himalayan and Andean mountains.

Not surprisingly, though, the group is most abundant in tropical regions. One of the richest localities I know, for instance, is a small outpost in Ecuador's Amazon basin called Santa Cecilia, where my colleagues and I once collected 56 different frogs in a single evening. A total of 81 species actually live there (precisely the number of frog species in the entire U.S.). Although the diversity of frogs at Santa Cecilia is unusually high, 40 or more species are commonly found in tracts of rain forest no bigger than two square kilometers.

But the frogs of Santa Cecilia are noteworthy for another reason: they epitomize a key trend in frog evolution, notably the movement away from water, toward land. Of the 81 species we found there, 35 are terrestrial during one or more developmental stages. Yet their proclivity for life on land belies a fundamental requirement of the group: amphibian eggs—like those of fishes—must be kept continuously moist because the semipermeable egg membrane offers little protection against desiccation. Moreover, virtually all males (like fishes) lack an intromittent organ, or penis, and thus must inseminate the eggs externally, after they pass from the female's cloaca (the combined reproductive and excretory opening).

Such a feat is accomplished when the male grasps the female (generally

WILLIAM E. DUELLMAN took the opportunity to study frogs when he was a student at the University of Michigan. Through this work he acquired a lifelong interest in frogs and their reproductive biology. After obtaining his Ph.D. at Michigan, he joined the faculty of the University of Kansas, where he is professor in the department of systematics and ecology, curator of the division of herpetology in the Museum of Natural History and director of the Center for Neotropical Biological Diversity. His field studies have taken him throughout North and South America and to Africa and Australia. His studies have resulted in some 250 publications, including *Hylid Frogs of Middle America* and, with Linda Trueb, *Biology of Amphibians.*

MATING FROGS of the genus *Centrolene* were photographed in Colombia. Their popular name, which derives from their transparency, is glass frogs; at the right the transparency makes the female's eggs visible. The eggs (*below*) develop on leaves above streams.

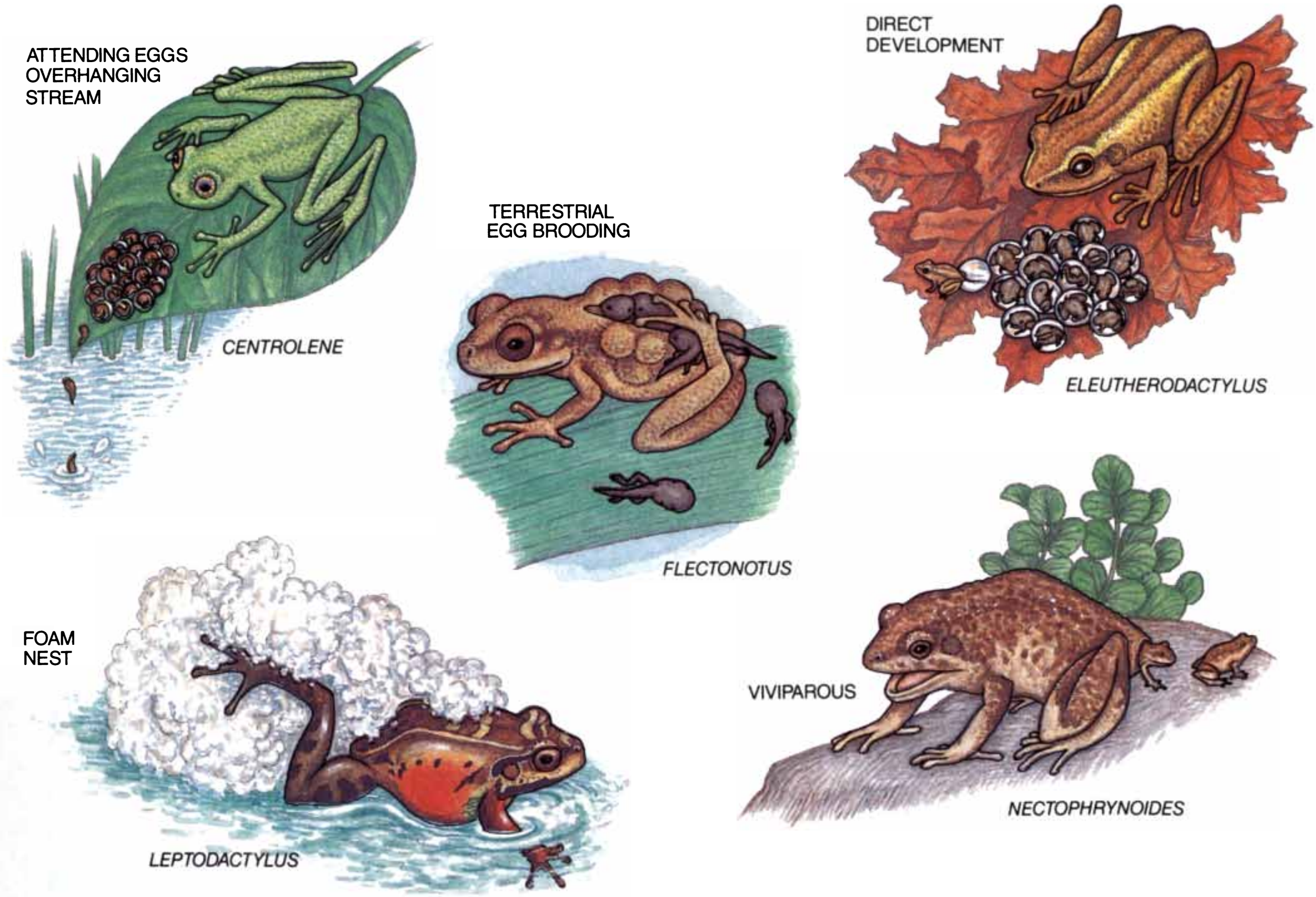
around her armpits) in a mating embrace known as amplexus. In most temperate species, mating takes place in the water, and so the egg clutch (and the aquatic tadpoles that hatch subsequently from it) is never at risk of desiccation. The situation is considerably different on land, however, where rainfall is not guaranteed and humidity levels may fluctuate.

In view of such physiological constraints, how is it frogs have colonized land so successfully? And why, given the harsh conditions that prevail on land, has it been evolutionarily advantageous for them to do so? The answer to the first question has several parts. To begin with, most terrestrial frogs inhabit tropical rain forests, where high humidity levels (close to 90 percent) reduce the risk of dehydration and where ambient air temperatures (25 to 30 degrees Celsius on average) foster rapid growth.

More significant perhaps is that terrestrial frogs adhere to surprisingly few stereotypes; during the 200 million years since their debut, they have evolved numerous—and in many cases startling—adaptations for life on land. Because many of these adaptations have arisen multiple times, they are construed to have a powerful selective advantage. Finally, it should be said that life on land does not necessarily imply life without water; many species lay their eggs in the small, temporary pools that form after a heavy rain or in places such as the spray zone of waterfalls where the humidity is exceptionally high. Thus, they are not terrestrial in the strict sense of the word.

The second question is harder because it is not so easily proved. Nevertheless, most herpetologists believe land offers a reprieve from aquatic predators such as the fishes and insects (and their aquatic larvae) that abound in tropical ponds and streams. The problem is most acute during the egg stage, when mortality may reach as high as 100 percent. Rich in protein and polysaccharides, the frog's membranous egg capsule provides prize fodder for an abundance of predators. According to my colleague Linda Trueb of the University of Kansas, frogs have achieved the best of both worlds: by adapting to land, they have reduced the risk of predation, yet by retaining the ability to live in water, they are able to move as conditions change. The jumping hind legs, of course, enable adults to change habitats quickly, and the muscular tail of some tadpoles allows them to wriggle across the ground.

In fact, many species complete only the egg stage on land, returning to water as tadpoles. In short, adaptive strategies among terrestrial frogs cover a broad gamut of behaviors. One of the simplest and most common calls for laying eggs near water. Indeed, egg clutches are often seen glued to the



REPRODUCTIVE TACTICS of frog species vary widely; some border on the improbable. In this depiction the genus name appears at the lower right of each panel, and the reproductive strategy is summarized at the upper left. One of the most un-

rocks and vegetation that overhang a tropical pond or mountain stream; from this vantage, the tadpoles drop neatly into the water when they hatch. All leaf frogs and glass frogs (so called because the skin on their ventrum, or underside, is transparent) lay their eggs in this fashion. Other species deposit their eggs in shallow depressions adjacent to ponds; when the nest floods, the tadpoles wash directly into the larger body of water.

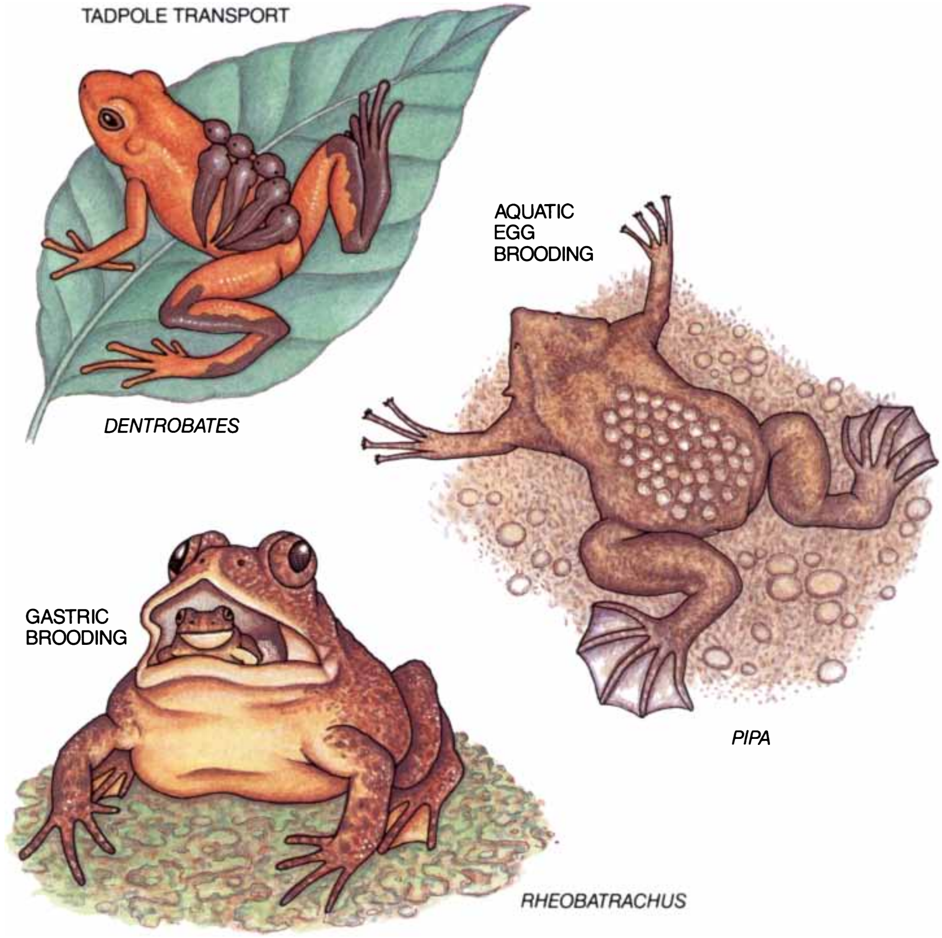
A more sophisticated alternative, which has been documented in at least four families, is to envelop the eggs in protective foam. As the eggs are laid, one or the other parent vigorously kicks its hind legs, mixing together air, sperm, eggs, cloacal secretions and sometimes water. When the frothy mass dries, its exterior turns tacky (sometimes hard) and so protects the eggs from physical harm. At the same time, the egg-filled interior remains liquid for as long as 10 days, which enables the eggs to survive short bouts of drought.

Strategies for laying eggs on land may lead to increased survivorship within the clutch, but they clearly have no effect on mortality during the aquatic tadpole stage. Indeed, predation pressure operating at the tadpole level probably explains another trend in frog biology: the shift away from streams and ponds to small pools or puddles that contain water for only a few days or weeks at a time. Such temporary pools often form in tree holes, at the base of arboreal plants called bromeliads or in small cavities in the ground. Because these water pockets are too ephemeral to support a predator population, they provide a comparatively safe environment in which all stages of the frog's life cycle can unfold. The great risk, of course, is that the water will evaporate before the eggs hatch or the tadpoles complete their development, in which case the entire clutch perishes.

A more derived evolutionary strategy involves prolongation of the egg stage. Rather than producing eggs that hatch into free-living tadpoles, some frogs lay eggs that hatch into four-legged froglets. Known as direct development, the process significantly reduces mortality, although fewer eggs are produced because each embryo needs a large quantity of yolk to see it through the long maturation period. Direct development is associated with nine families of frogs, including the immense tropical American genus *Eleutherodactylus* and related genera; it also occurs in many Australian, Asian and African species. In fact, the elimination of a free-living, feeding tadpole stage is characteristic of nearly 800 frog species—20 percent of the species known.

Although most direct-development frogs live in rain or cloud forests, one of the more interesting but poorly understood genera of this kind is *Breviceps,* the African rain frog. As the name suggests, the animal comes above ground only during heavy downpours. Although much about the life history of this elusive animal remains undocumented, the adults are known to form pairs during the breeding season. Adults emerge from their underground burrows and absorb rainwater through the skin, thus replenishing fluid in their bladder and other body tissues.

Because of his comparatively diminu-



usual strategies is found in the Australian genus *Rheobatrachus:* after the male has fertilized the eggs, the female swallows them and broods them in her stomach.

tive size, the male cannot achieve amplexus with the larger, rotund female but instead glues himself to her back. With the male riding on her back, the female burrows into the ground and proceeds to lay eggs that are then fertilized by her amplectic partner. Periodically the female wets the eggs with water from her bladder, keeping them moist until they hatch as froglets. Most species of *Breviceps* are true desert dwellers, living in the arid regions of sub-Saharan Africa, and one (*B. macrops*) inhabits coastal sand dunes, on the Atlantic coast of South Africa, where there is no fresh water.

Some species undergo a form of highly specialized direct development known as viviparity. Literally meaning live birth, viviparity occurs when the eggs are retained inside the female, hatching as advanced tadpoles or froglets after a period of incubation more reminiscent of mammals than of amphibians. Although energetically taxing for the female, viviparity protects the young against terrestrial predators and profoundly influences the chances of survival.

Viviparity has been documented in only five species of frogs (of those, four belong to the same genus), but the number is bound to increase as biologists learn more about the life history of tropical anurans. In three—*Eleutherodactylus jasperi* from Puerto Rico and *Nectophrynoides tornieri* and *N. viviparus* from Africa—the tadpoles rely solely on egg yolk for their development and so are considered ovoviviparous (meaning live birth from eggs). True viviparity, in which the female supplements yolk with secretions from her oviduct, giving birth to newly metamorphosed froglets, is known to occur in only two African species: *N. liberiensis* and *N. occidentalis.*

Parental care, the range of behaviors exhibited by individuals protecting their offspring, is well documented among birds and mammals, but it is also unexpectedly common among frogs. As with other animals, parental care among frogs typically involves one or both parents. Some species display only rudimentary behavior, as in the case of the African hairy frog (so named because males grow long, hairlike extensions of the epidermis when breeding), which simply sits on its egg clutches in water, but by doing so protects them from aquatic predators such as insect larvae and fish. Or parental care may be more energetically costly, as in the case of the small African toad, *Nectophryne afra,* the male of which stays with its eggs throughout their development, kicking his feet in the water near the eggs and thus increasing oxygen flow through the membranes. Among more specialized frogs, care ranges from retention of the young before they hatch (as in viviparous species) to the transportation, feeding and incubation of the young after they hatch.

Males act as guardians of the offspring in some species; in others the females do. In only a few are both sexes known to cooperate as providers for their young. Peter Weygoldt of Albert-Ludwigs University in Germany studied a captive laboratory population and reported seeing a most unusual form of cooperation among males and females of *Dendrobates pumilio,* a small dart-poison frog from Costa Rica. In this species the two sexes divide parenting duties: males guard the eggs for the first 10 to 12 days until they hatch; thereafter females assume care for the young. The females begin by transporting each newborn tadpole to a bromeliad, at the base of which a small pool of water has collected. Although protected from desiccation and predation, the tadpole has no food supply and therefore relies entirely on its mother for nutrition during the six- to eight-week period to metamorphosis. The mother accommodates her offsprings' needs by returning periodically to each bromeliad to deposit an unfertilized egg, which provides the tadpole with essential proteins and carbohydrates [see "Dart-Poison Frogs," by Charles W. Myers and John W. Daly; SCIENTIFIC AMERICAN, February 1983].

Progressive provisioning of this type has subsequently been reported in other dart-poison frogs, both in the laboratory and in the field. It has also been observed in the large Jamaican tree frog, *Osteopilus brunneus,* which like *Dendrobates* deposits its eggs in bromeliads. Leaf frogs (so named because many species encase their eggs in leaves) have evolved a distinctly different strategy. At the time they deposit the egg clutch, female leaf frogs also lay many eggless, water-filled capsules. Although the capsules have no nutritive value, they are a vital source of water, which reaches the eggs by osmosis.

In some species the task of parental

FOAM NEST of the gray tree frog, genus *Chiromantis,* is visible below the two mating pairs in the photograph at the left. The foam serves to protect the eggs. At a later stage (*above*), tadpoles are seen dropping from the foam nest into the water below. The photographs were made in South Africa.

care falls to the males, who aggressively defend their eggs against a variety of predators. The aptly named gladiator frogs, for instance, frequently engage in violent territorial disputes with other males, wielding needlelike spines at the base of the thumb to slash the skin and eardrums of any intruder. In this species the males invest considerable time and energy in their offspring, initially by forming nests in which the fertilized eggs will be laid and subsequently by staying with the eggs until they hatch.

MOUTH BREEDING by the adult male is part of the reproductive strategy of Darwin's frog, *Rhinoderma darwinii*. The male takes the newly hatched tadpoles into his mouth; they move into his vocal sacs and stay there for several weeks until their development is complete. Developed tadpoles have just emerged from the mouth of this male, photographed in Chile.

Males create the nests by scooping mud from banks adjacent to slow-moving streams or ponds, thus forming shallow basins that fill with water. The resulting predator-free site has the advantage of being close to a permanent body of water but is nonetheless risky because the eggs, which are deposited as a thin film on the water's surface, are vulnerable to attack. Any rupture in the egg film, brought about, say, by the leap of another frog or the aerial dive of a dragonfly, will cause the eggs to sink to the bottom, where they die from lack of oxygen. Consequently, males vigorously defend their eggs and rush to head off any intruder.

Other species forcefully defend their calling sites (which may include egg deposition sites). In Tandayapa, Ecuador, for example, I have seen *Centrolene* males spring into action when approached by conspecifics (males of the same species). Thus confronted, they grapple, attempting to dislodge one another from a favored leaf overhanging a stream. Males of the Australian tusked frog, *Adelotus brevis,* also engage in battles. Equipped with long, pointed tusks that protrude from the lower jaw, they jump and snap at intruders.

Not all males are so confrontational. In some species, males carry the eggs with them until they hatch and so have no need to defend a nest site. Such behavior was first observed more than 200 years ago, when males of the midwife toad (appropriately named *Alytes obstetricans*) were found with strings of eggs entwined around their hind legs. Since then, egg transport has been documented in at least eight families of frogs and has been noted in both males and females. It ranges from simple piggybacking (when the eggs or tadpoles adhere to the parent's back) to egg brooding (when the eggs develop in a special pouch somewhat analogous to the marsupial mammal pouch).

Although egg brooding is most common among females, in the minute Australian hip-pocket frog, *Assa darlingtoni,* it is the males who brood the young. Shortly after hatching, the tadpoles wriggle up their father's legs and into special lateral pouches, where they continue their development. In other species, males play a facilitating role during mating, guiding the eggs to the female. In the South American frog *Pipa,* for example, egg laying is accompanied by a truly graceful display of underwater acrobatics: as the swimming pair flips and turns, the male spreads the emerging eggs across his partner's back, where they adhere to her skin. In some species the skin then swells, enveloping the eggs in a protective matrix. After spending about two months thus embedded in the female's back, the tadpoles—or in some species tiny froglets—burst through the skin to become free-living frogs.

One of my favorite examples of egg brooding occurs among South American tree frogs in the family Hylidae. Indeed, because the frogs brood their eggs in a manner analogous to that of mammals, they are often referred to as the marsupial frogs. The analogy stems from the presence of a unique epidermal pocket on the back of the female. As the eggs are extruded and fertilized, they are immediately pushed into the pouch by the male who propels them across the female's back with his feet. Once inside the pouch, the eggs develop special gill-like structures that exchange oxygen and carbon dioxide osmotically with the highly vascularized tissues lining the pouch, enabling the embryos to breathe.

In most species the eggs hatch as froglets, which then drop off the mother's back or crawl from her pouch. But in some species of *Gastrotheca* living at high elevations in the Andes, development terminates at the tadpole stage; the female sits in shallow ponds and releases her tadpoles into the water. The stage at hatching is determined by the amount of yolk present in each egg, which in turn reflects the number of eggs produced per clutch. Species in which the eggs hatch as small tadpoles produce 100 or more ova, each about two millimeters in diameter. Direct-development species may produce only six ova, but each is about 10 millimeters in diameter [see "Marsupial Frogs," by Eugenia M. del Pino; SCIENTIFIC AMERICAN, May 1989].

Whereas the number of eggs tends to reflect clutch size, development time mirrors climate conditions. Frogs throughout the tropics, for example, develop relatively rapidly, sometimes spending only two or three weeks in the tadpole stage, whereas those that live in cool, temperate climates develop much more slowly. One such species is the spotted frog, *Rana pretiosa,* which lives in the cold streams that cascade down the Rocky Mountains. Because the cold water in which the frogs live slows their metabolism, more than one year is needed to produce fully yolked eggs, and females lay eggs only once every two or three years.

Tadpoles, too, metamorphose slowly. Populations of bullfrogs, *Rana catesbeiana,* living in the northern U.S. and Canada, typically spend two years in the tadpole stage; another species, *Ascaphus truei,* needs three years to reach

TRANSPORT OF TADPOLES takes place on the back of a female dart-poison frog, *Dendrobates reticulatus,* in the Amazon rain forest of Peru. This female is carrying two tadpoles side by side. Once she gets them to water, often in a temporary pool formed at the base of the type of arboreal plant called a bromeliad, she will feed them with unfertilized eggs for about six weeks.

MARSUPIAL FROGS get their name from the pouch on the back of the female. As eggs are fertilized, the male pushes them into the pouch, where they develop to the tadpole or froglet stage. Three newly born young are shown with their mother, and another is shown at birth from this female's pouch. She is a marsupial frog of the species *Gastrotheca ovifera* and was photographed in Venezuela.

adulthood. Although bullfrogs are enormously fecund, producing from 10,000 to 20,000 eggs per year, mortality during the long development period is also extremely high, reaching as much as 99 percent.

In arid habitats, development is limited not by temperature but by moisture. Desert-dwelling frogs such as *Breviceps* may breed only on one or two nights a year, when it rains heavily. But once fertilization occurs, growth proceeds rapidly. Spadefoot toads in the southwestern U.S., for example, dispense with the tadpole stage in less than two weeks, a pace deemed necessary in a habitat where water may last for only a few weeks. Frogs in comparable habitats elsewhere in the world show similar patterns.

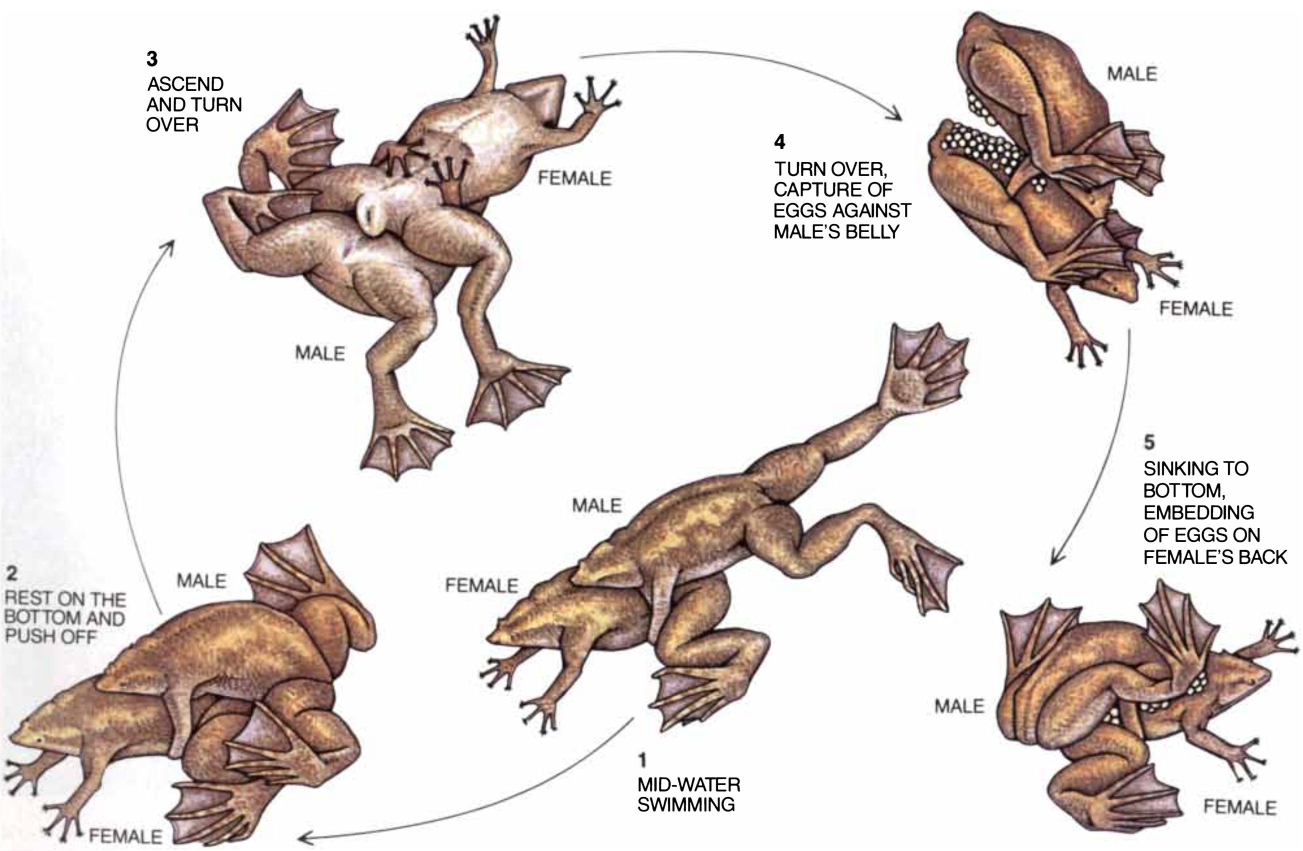
Fascinating as such diverse life-history strategies are, few would be scientifically documented were it not for the willingness of herpetologists to spend countless hours observing frogs under natural field conditions. Indeed, I am often asked why I choose to spend so much time wandering through the world's jungles at night looking for snakes, frogs and other cold-blooded vertebrates. Yet the answer is obvious, I think, to any field biologist: the natural world offers an endless cornucopia of wonderment and surprise. My colleagues and I never know, for example, when something unique will suddenly appear in the beam of our headlamps, even though we might be walking along a trail that we have traversed a dozen nights in succession. Perhaps we will find a species we have never seen before; perhaps we will come across a species no one has ever seen before.

One of the most thrilling moments of my life, in fact, took place during an expedition to southern Chile in 1975. One day I came across Darwin's frog, *Rhinoderma darwinii,* just as it was giving "birth." Although the frog is small and rather drab, it has evolved a mode of development unlike any ever described. Adult males take the newly hatched tadpoles into their mouth, and from there the young migrate to the vocal sacs. They remain for several weeks until growth is complete and then emerge from the father's mouth.

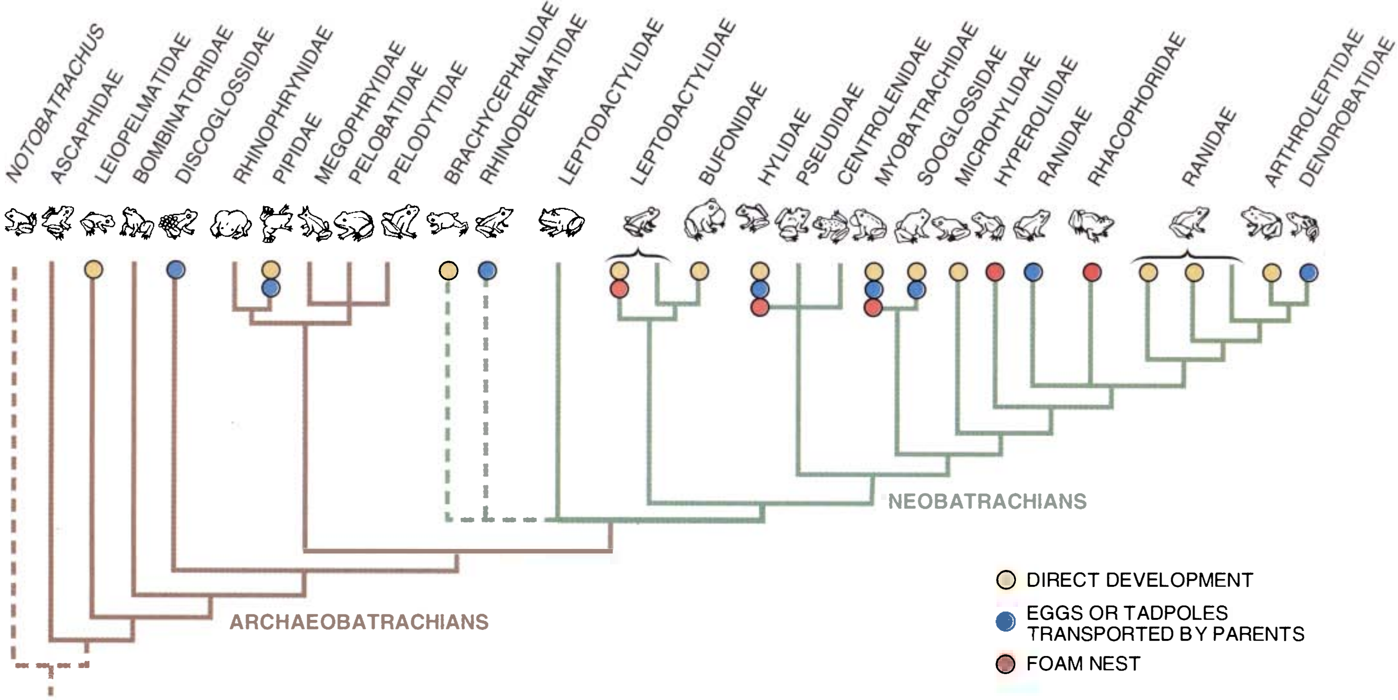
I was aware that *Rhinoderma* engaged in such behavior but nonetheless was excited beyond words to see it finally for myself. In fact, soon after witnessing a succession of froglets parade from their father's mouth, I dashed a letter off to Michael J. Tyler, a colleague and fellow frog enthusiast at the University of Adelaide in Australia. Imagine my chagrin a few weeks later when I received a reply that put my small announcement to shame. Tyler and his colleagues C. J. Corben and G. J. Ingram had recently observed a previously unknown yet more bizarre form of parental care in an Australian frog, *Rheobatrachus silus.* In that species, it is the females who swallow the eggs after fertilization and then brood them in the stomach. A photocopy of the paper detailing the discovery was inscribed simply, "Touché! Mike." My small observation had clearly been overshadowed.

Gastric brooding, as the phenomenon is called, ranks as one of the strangest examples of animal reproduction known. Having finally observed these frogs for myself in 1979 while visiting southern Queensland, I can truthfully say that *Rheobatrachus* has evolved a reproductive mode unlike any other frogs. Who would believe that tadpoles could spend six weeks in their mother's stomach without being digested? How is such a feat possible?

To begin with, nurturing females



MATING PROCEDURE of the South American frog *Pipa carvalhoi* gives rise to graceful underwater acrobatics. With the male riding on the female, the pair flips and turns, and the male spreads the emerging eggs across the female's back. There they adhere and become embedded in a swelling of the skin, hatching two months later as tadpoles or tiny froglets.



MAJOR FROG FAMILIES are classified according to their reproductive strategy (*colored circles*) and family relationships (*colored lines*). The broken lines in the diagram of family relationships represent associations that are questionable.

cease to feed during the breeding period. Tyler and his colleagues have shown that production of hydrochloric acid and pepsin are halted in the stomach by the hormonelike substance prostaglandin E_2, which is secreted first by the egg capsules and then by the tadpoles. With the shutting down of normal functioning in this way, the stomach is transformed from a digestive organ into a protective, gestational sac.

The eggs, which range in number from 21 to 26, are relatively large—about five millimeters in diameter—and therefore rich in yolk. Consequently, the tadpoles do not need an external source of nutrition but feed exclusively on yolk throughout their six-week developmental period. During birth, the female's esophagus dilates in a manner that recalls the birth of mammalian young through the vaginal canal, and the young froglets are propelled from her mouth. Within a few days after expulsion of the young, the stomach begins to function again as a digestive organ, and the frog resumes feeding.

In 1984 a second species of gastric brooder, *Rheobatrachus vitellinus,* was found farther north in Queensland. Sadly, intensive searching during the past few years has failed to turn up individuals of either species, leading my colleagues and me to conclude that both species are now extinct. The loss is especially unfortunate because preliminary studies by Tyler and his associates indicate that prostaglandin extracts from these species might have been effective in the treatment of human stomach ulcers.

After the discovery of gastric brooding and tadpole feeding, I would not be surprised by anything. But why is it that frogs demonstrate such reproductive plasticity when other vertebrates do not? All birds, for example, lay shelled eggs, and nearly all mammals bear living young that are then suckled by the female. Yet frogs conform to few if any reproductive stereotypes. Moreover, it is evident that their reproductive tactics are not the result of simple mutation but the outcome of complex physiological, morphological and behavioral interactions.

The fact that some members of the three amphibian groups (caecilians, salamanders and frogs), as well as fishes, deposit their eggs in water suggests aquatic egg laying is a primitive (generalized) trait. Other strategies, which have evolved independently in many lineages of frogs, therefore can be viewed as evolutionarily derived. One conclusion is certain: frogs, which seem distinctly unsuited for a terrestrial existence, have adapted in extraordinary ways to life on land and in doing so have managed to colonize much of the planet.

Is it not therefore ironic and terribly unfortunate that frogs, having radiated so successfully, are now experiencing extinction at unprecedented rates, victims of human inability to preserve the natural world? Within the past five years alone, an untold number of species have been lost, many to habitat destruction. Although the decline and extinction of anurans is not well understood, a number of biologists (myself included) think the cumulative effects of air and water pollution, acid rain and increased radiation brought about by the loss of stratospheric ozone are taking their toll. Regrettably, the loss of so many species not only affects the overall stability of ecosystems but brings to an end evolutionary lineages that have survived for millions of years. The magnitude of such loss is immeasurable. Our only hope is that people and their governments will recognize the consequences of biological extinction and take steps to prevent it before too much of our global gene pool is gone.

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