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Amphibian diversity and life history

Martha L. Crump

> When the first crossopterygian crawled out of the rich Devonian waters and cast the first envious vertebrate gaze at the terrestrial world, a boundless empire awaited colonization. Although the change from an ungainly lobe-finned locomotion to a terrestrial walking gait . . . was agonizingly slow, generations succeeded generations, archotypes [*sic*] gave way to new evolutionary experiments, and the land became the home for the first quadrupeds—the amphibians.
>
> William E. Duellman (1970)

1.1 Introduction

Over the past 350 million years, amphibian descendents of lobe-finned fishes have radiated into most habitats on Earth. In doing so, they have acquired spectacular and sometimes bizarre physiological, morphological, behavioral, and ecological attributes that mold their innovative life histories. Amphibians have highly permeable skin, which makes them both vulnerable to losing water and able to absorb water. Their eggs, covered with jelly capsules rather than hard shells, lose water rapidly. For these reasons, amphibians require relatively moist environments.

Many sampling techniques have been developed in North America or Europe where most amphibians exhibit the complex life cycle of aquatic eggs, aquatic larvae, and metamorphosis into terrestrial adults that return to water to breed. Not all amphibians fit this stereotype. The spectacular diversity of amphibian life histories provides a focus for studying their natural history, as well as presents a challenge since researchers must ensure that field methods are appropriate for the target species.

1.2 Amphibian species richness and distribution

Scientists have named approximately 1.75 million species of living organisms (Groom *et al*. 2006). About 72% of all named animals are insects; about 5% are vertebrates. Approximately 0.5% of all animal species—6347 species (see AmphibiaWeb; http://amphibiaweb.org)—belong to the class Amphibia. The class gets it name from the Greek words *amphi* meaning "two" and *bios* meaning "mode of life" because many species have a diphasic life history: they spend part of their lives in water and part on land. Biologists divide the class into three orders: Gymnophiona (caecilians), Urodela (salamanders), and Anura (frogs) (Figure 1.1).

Gymnophiona, from the Greek words *gymnos* and *ophis* meaning "naked serpent," encompasses 174 species. Caecilians, which resemble large earthworms, are long, skinny animals with no legs and reduced eyes. Annuli (grooves) encircle their bodies. Their tails are either greatly reduced or absent, and a sensory tentacle sits between each eye and nostril. Some caecilians have small dermal scales beneath the surface of their mucus-covered skin. These scales, composed mainly of collagen fibers and minerals, are not found in salamanders or anurans. Adult caecilians range in length from a little more than 10 cm to about 1.5 m. Most are highly specialized for burrowing. Others live on the ground but are cryptic and secretive. Some are aquatic. Caecilians occur in tropical habitats around the world except for Madagascar and the Papuan–Australian region (Pough *et al.* 2004).

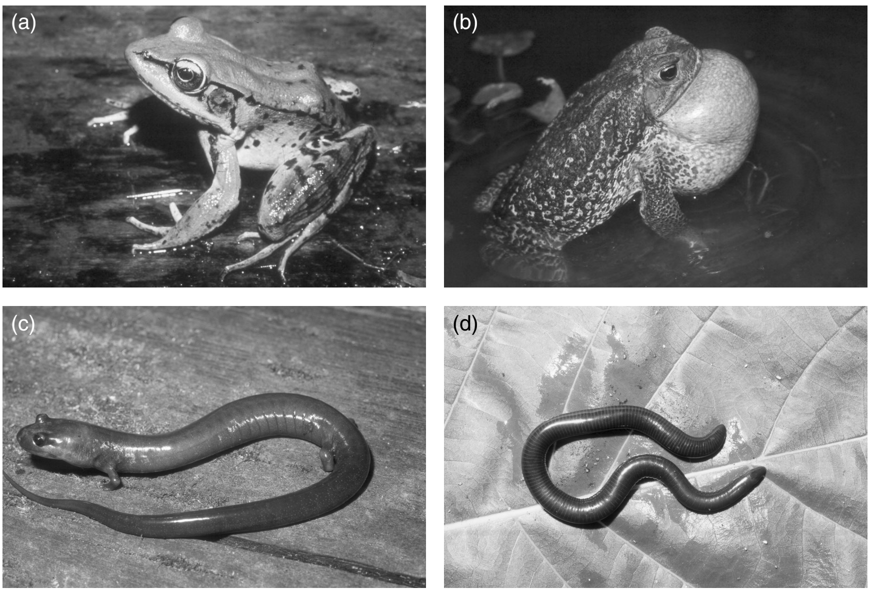

Fig. 1.1 Representatives of the three orders of amphibians. (a) Anura: *Rana palmipes*, from Ecuador, (b) Anura: *Bufo arenarum*, from Argentina, (c) Urodela: *Phaeognathus hubrichti*, from Alabama, USA, (d) Gymnophiona: *Hypogeophis rostratus*, Seychelles. Photographs (a) and (b) by Martha L. Crump; photographs (c) and (d) by C. Kenneth Dodd, Jr.

Five hundred and seventy-one species belong to Urodela, from the Greek words *uro* and *delos* meaning "tail evident." All salamanders have tails, and adults have elongate bodies. Most have front and back legs of about the same length; the limbs of a few aquatic species are greatly reduced or absent. Salamanders are completely aquatic, terrestrial, combined aquatic and terrestrial, fossorial, or arboreal. Adults range in size from about 30 mm to nearly 2 m. Most salamander species occur in eastern and western North America and temperate Eurasia, although plethodontids have radiated extensively in Central and South America. There are no salamanders in sub-Saharan Africa, Australasia, Australia, or much of tropical Asia, and they are missing from most islands (Pough *et al.* 2004).

Frogs, which include toads, make up the order Anura from the Greek words *an* and *oura*, meaning "without tail." Although tadpoles have tails, adults do not. Anurans live in the water, on the ground, underground, and in the trees. Most have long, strong back legs well suited for jumping. Males of most species call to attract females for mating. Adults of the 5602 recognized species range in size from about 13 mm to 30 cm. Anurans live almost everywhere except where restricted by cold temperatures or extremely dry conditions, and except for many oceanic islands (Pough *et al.* 2004).

Duellman identified 43 areas worldwide with exceptionally high numbers of amphibian species, endemic species (those found nowhere else), or both (Duellman 1999). Nineteen of these high diversity areas are in the western hemisphere; the others are in Eurasia, Africa, and the Papuan–Australian region. The neotropical region houses 54% of the world's amphibian species.

Amphibians live in nearly every habitat except for open oceans, most oceanic islands, polar regions, and some extremely dry deserts (Wells 2007). These restrictions are imposed on them because of their highly permeable skin that loses water, and because they are ectothermic: the energy needed to raise their body temperatures comes from the sun. Thus, amphibians become inactive at low temperatures. These characteristics, however, work to their advantage as well. In dry areas and those with seasonal rainfall, amphibians absorb water through their skin by contacting moist soil. Their low metabolic rates translate into low energy requirements and allow them to estivate, often underground, during unfavorable conditions.

1.3 Amphibian lifestyles and life history diversity

Textbooks, management guides, and monitoring manuals, especially those originating in Europe and North America, often give an oversimplified impression of amphibian life histories. In fact, amphibian life histories are often complex, and many are still poorly understood. Not all species have an aquatic larval stage and a terrestrial adult stage.

Reproductive mode, a central aspect of amphibian life history, refers to the site of egg deposition, egg and clutch characteristics, type and duration of embryonic and larval development, and type of parental care if any (Duellman and Trueb 1986). Many amphibians are not tied to aquatic habitats for reproduction. Instead, they reproduce on land, underground, or in trees, even in the temperate zones. The following brief discussion of selected lifestyles and life histories reveals that similar behaviors have evolved in diverse taxonomic groups and geographical areas: amphibian "experiments" toward greater independence from standing or flowing water and perhaps from lower predation pressure as well.

Readers wishing more information concerning amphibian life histories should consult Duellman (2007) and Wells (2007). For reviews of reproductive modes, see Salthe (1969), Salthe and Duellman (1973), Wake (1982, 1992), Haddad and Prado (2005), and Duellman (2007). For reviews of parental care see Crump (1995, 1996).

1.3.1 Caecilians

Caecilian lifestyles include aquatic, combined aquatic and terrestrial, terrestrial, and fossorial. Fully aquatic caecilians generally have compressed bodies with well-developed dorsal fins on the posterior portion. Fossorial species generally have blunt heads, used for pushing and compacting the soil while burrowing.

Although details of reproductive biology are unknown for many species, caecilians display two basic modes: oviparous (egg-laying) and viviparous (bearing live young) (Wake 1977, 1992). Oviparous caecilians lay eggs on land. In some species the eggs hatch into larvae that wriggle to water. Caecilian larvae exhibit less dramatic metamorphosis than do salamanders or frogs. They hatch almost fully developed, and the larval period is short. The eggs of some oviparous species undergo direct development. That is, development occurs within the egg capsule; there is no free-living larval stage. Some oviparous females stay with their eggs, which probably protects them from predators and from drying out. Viviparity evolved independently several times in caecilians. Females retain eggs in their oviducts until development is complete (Wake 1993; Wilkinson and Nussbaum 1998). After the developing young exhaust their yolk reserves, they scrape lipid-rich secretions from their mothers' oviductal epithelium with their fetal teeth. Gestation lasts for many months, and the newborn are large relative to their mothers.

1.3.1.1 Aquatic

All species in the South American family Typhlonectidae are either fully aquatic or semi-aquatic. Some in the latter group spend the day in burrows they construct next to water, then emerge at night to feed in shallow water. All typhlonectids are assumed to be viviparous. Soon after the young are born, they shed their gills and quickly acquire adult morphology.

1.3.1.2 Combination aquatic and terrestrial

Caecilians of the two most primitive families—Ichthyophiidae and Rhinotrematidae—all appear to have complex life cycles encompassing both water and land. As far as is known, ichthyophiids from southeastern Asia lay their eggs in burrows or under vegetation at the edge of water. The female coils around her eggs. The hatchling larvae wriggle to water. Rhinotrematids from South America likewise appear to be oviparous, and free-living aquatic larvae have been found for some species. Although egg-laying sites are unknown, females presumably oviposit on land near water and the larvae make their way to water. The developmental mode is not known for uraeotyphlids, from southern India, but presumably they also lay eggs on land and have aquatic larvae. Some species of the large, widespread family Caeciliidae also oviposit on land and have free-living aquatic larvae.

1.3.1.3 Terrestrial and/or fossorial

Many caecilians burrow underground, although some forage at night on the ground surface. Some terrestrial and fossorial caeciliids from South America, Africa, India, and the Seychelles lay direct-developing eggs. In some of these, females have been found coiled around their eggs. Some terrestrial and fossorial caeciliids are viviparous. All members of the family Scolecomorphidae from Africa are terrestrial. One is viviparous; in the other five species the mode is unknown.

1.3.2 Salamanders

Salamander lifestyles include fully aquatic, combined aquatic and terrestrial, terrestrial, arboreal, and fossorial. Body shapes of aquatic salamanders range from the slender and eel-like sirenids and amphiumids to the flattened and robust cryptobranchids. Many permanently aquatic species retain external gills as adults. Most arboreal salamanders are small and have extensively webbed feet; some have prehensile tails. Burrowing salamanders generally have long slender bodies and tails, reduced limbs and feet, and small body size.

As a group salamanders exhibit diverse reproductive modes. Some salamanders go through a complex life cycle with aquatic larvae and metamorphosis. Others are paedomorphic: they become sexually mature and reproduce while retaining juvenile characteristics. Still others have direct-developing eggs or give birth to live young.

1.3.2.1 Aquatic

Some aquatic salamanders lay eggs in still or slowly flowing water. *Siren* and *Pseudobranchus* from southeastern USA and northeastern Mexico live in swamps, lakes, marshes, and sluggish streams, where they attach their eggs to vegetation. The larvae develop into eel-like paedomorphic adults: they lack eyelids, have external gills, and their skin resembles larval skin. When their habitat dries out, sirenids secrete a mucous cocoon and burrow into the mud where they estivate until conditions improve. The Mexican axolotl (*Ambystoma mexicanum*) is permanently aquatic and paedomorphic. Its larvae fail to metamorphose fully, and the gonads mature in the larval body form.

Proteus anguinus, from southeastern Europe, lives in subterranean lakes and streams of limestone caves where it lays aquatic eggs that hatch into aquatic larvae. Females attend their eggs. In North America, *Typhlomolge* and *Haideotriton* also live in cave waters and lay aquatic eggs that hatch into aquatic larvae. All these species are paedomorphic.

Some aquatic salamanders oviposit in flowing water of cold streams. Male hellbenders (*Cryptobranchus alleganiensis*) from eastern North America construct nests under rocks. More than one female might lay her strings of eggs in the nest. The male guards the eggs through their early stages. Likewise, male *Andrias japonicus* from Japan and male *Andrias davidianus* from central China guard their nests. In all three cryptobranchid species, aquatic larvae undergo incomplete metamorphosis. The adults retain certain larval features such as lidless eyes and the absence of a tongue pad.

1.3.2.2 Combination of aquatic and terrestrial

In Eurasia, many salamandrids (e.g. *Triturus*) live on land but lay their eggs in ponds, lakes, or streams. Likewise, most Asian hynobiids are terrestrial as adults but migrate to aquatic sites to lay aquatic eggs that hatch into aquatic larvae. The same is true for many North American terrestrial salamanders. Tiger salamanders (*Ambystoma tigrinum*) and spotted salamanders (*Ambystoma maculatum*) migrate to breeding ponds in the spring. Once the aquatic larvae metamorphose and leave the water, they return to their aqueous beginnings only during breeding season.

In contrast, female marbled salamanders (*Ambystoma opacum*) lay their eggs under leaf litter or logs in depressions on dry ground. They stay until their eggs hatch when the nests flood during winter rains. Following aquatic larval development and metamorphosis, marbled salamanders are completely terrestrial.

Female *Amphiuma* from the southeastern USA lay large yolky eggs in dried-out swamps or in cavities under logs near ponds: places that will flood during spring and summer rains. Females stay with their eggs until then. Once they hatch, the well-developed larvae metamorphose within a few weeks. Adults live in swamps or slow-moving streams, but move overland during rains. They survive droughts by burrowing underground for 2 years or more.

Some plethodontid salamanders lay eggs on land, and after hatching the larvae make their way to water. Female *Hemidactylium scutatum* oviposit just above or at the water line in bogs and swamps. After hatching, the larvae wriggle or flip into the water. Some *Desmognathus* lay their eggs under rocks, logs, or leaf litter at water's edge. The newly hatched larvae stay with their mother in the nest site for several days, then wriggle to water.

The complex life cycle of red-spotted newts (*Notophthalmus viridescens*) from eastern North America involves several stages. Aquatic females attach their eggs to underwater vegetation. The eggs hatch into aquatic larvae that eventually metamorphose into an immature terrestrial stage called an eft. The orange-red efts stay on land for 1–14 years. Eventually they return to ponds where they turn dull green with a row of small red dots along each side of their body and transform into the aquatic adult body form. In some populations, however, paedomorphic adults reproduce in the larval body form.

1.3.2.3 Terrestrial

Many species of salamander live under leaf litter or logs, retreating into crevices or holes during dry conditions. Terrestrial salamanders, including many in the temperate zone, have various ways of reproducing independent of water bodies. The seepage salamander (*Desmognathus aeneus*) oviposits in a nest near water. The larvae hatch at an advanced stage and metamorphose within a few days in the nest without feeding. Other plethodontid salamanders (e.g. *Desmognathus wrighti*, *Bolitoglossa*, and *Plethodon*) lay large, direct-developing eggs in cavities or inside hollow logs. In many species, the female remains with the eggs; in a few species the male remains instead. Montane populations of European fire salamanders (*Salamandra salamandra*) often retain eggs in their oviducts. The young absorb nutrients from their yolk and are born live, although lowland populations usually have aquatic eggs and larvae. *Salamandra atra* are viviparous; after the developing young exhaust their yolk reserves, they obtain nutrients from the female.

1.3.2.4 Fossorial

Most *Oedipina*, fossorial or semi-fossorial plethodontid salamanders ranging from Mexico to northern South America, lay direct-developing eggs underground. Some fossorial plethodontids (e.g. *Lineatriton lineola*) attend their direct-developing eggs.

1.3.2.5 Arboreal

Neotropical arboreal plethodontids (e.g. *Bolitoglossa* and *Nototriton*) lay their eggs under mats of mosses and liverworts on tree branches and in bromeliads. The eggs undergo direct development, and some female *Bolitoglossa* attend their eggs. *Aneides lugubris* from western North America lays direct-developing eggs as high as 10 m above the ground.

1.3.3 Anurans

Anuran lifestyles include purely aquatic, aquatic and terrestrial, terrestrial, arboreal, and fossorial. A frog with relatively short hind legs is most likely a terrestrial hopper or fossorial species. One with long hind legs is likely to be aquatic, arboreal, or a jumping terrestrial species. Aquatic anurans tend to have their eyes on the top of their heads rather than at the sides, and they often have fully webbed feet. Some have flattened bodies. Arboreal frogs generally have expanded pads on the ends of their toes. Many fossorial species have small heads with pointed snouts and depressed bodies. Some have spadelike tubercles on their hind feet used for burrowing.

Anurans have evolved remarkably diverse life histories, from aquatic eggs to viviparity. In between those extremes, frogs from numerous families on many continents lay their eggs out of water yet have aquatic larvae. In the section headings below, the first designation refers to post-metamorphic stages, the second to egg and/or larval stages.

1.3.3.1 Aquatic/aquatic

Many aquatic frogs lay eggs that hatch into tadpoles. African clawed frogs (*Xenopus*) attach their eggs to submerged vegetation in standing water. The South American paradox frog (*Pseudis paradoxa*) oviposits among vegetation in shallow water of ponds and lakes. Aquatic larvae grow to 25 cm—the largest of any frog—then they metamorphose into relatively small juveniles. Tailed frogs (*Ascaphus truei*) from northwestern USA and adjacent Canada live in cold, torrential streams where they lay eggs under rocks. In some areas larvae require several years to metamorphose.

Some fully aquatic anurans brood their young. Female South American *Pipa* carry eggs embedded in their backs. In some species of *Pipa* the eggs hatch into tadpoles. In others they undergo direct development. Female Australian gastric-brooding frogs (*Rheobatrachus*) swallowed their late-stage eggs or early-stage larvae, and the tadpoles absorbed yolk reserves while developing in their mothers' stomachs. No *Rheobatrachus* have been seen since the 1980s; both species are assumed extinct.

1.3.3.2 Terrestrial/aquatic

Terrestrial anurans from many families lay aquatic eggs, and the aquatic larvae metamorphose into terrestrial juveniles. Species that oviposit in standing water produce clutches in compact masses (some ranids), floating rafts on the water surface (some ranids), strings (most *Bufo* and some pelobatids), scattered individually or in small packets on the bottom substrate (*Bombina* and *Discoglossus*), attached individually or in small groups onto submerged plants (some species of *Pseudacris*, *Acris*, *Hyla*, and *Spea*), or as a film on the water surface (some microhylids).

Some anurans breed in moderately fast streams or mountain torrents. Female *Atelopus* from Central and South America lay their eggs in strings attached to rocks. The larvae have ventral sucker-like discs that allow them to adhere to rocks while feeding. Tadpoles of bufonid stream-breeding *Ansonia* from Asia and *Werneria* from Africa have similar suckers. Other stream-adapted frogs, such as many ranids, lay large eggs in compact masses attached to rocks in areas where the current is slow and the eggs are less likely to be swept away.

Some terrestrial anurans produce foam nests in which their eggs are suspended. Male *Leptodactylus*, *Physalaemus*, and *Pleurodema* from Central and South America kick their hind legs during amplexus, whipping the females' eggs and mucus and their sperm and mucus into foamy masses (Figure 1.2a). The outermost layer of foam dries quickly and provides some protection against desiccation and predation. Some foam-nesters produce their nests on the water surface, others in cavities or holes next to ponds. *Leptodactylus bufonius* constructs mud nests at the margin of temporary ponds and deposits its foam nests inside (Figure 1.2b). The eggs hatch into tadpoles that remain in the nests until rains dissolve the nests and flood the area. Some Australian myobatrachids also construct foam nests on the water surface.

Some terrestrial frogs oviposit in very small bodies of water on land. Brazilian *Bufo castaneoticus* lay their eggs in water-filled fruit capsules of the Brazil nut tree, and the tadpoles feed on detritus. *Eupsophus* from Chile and

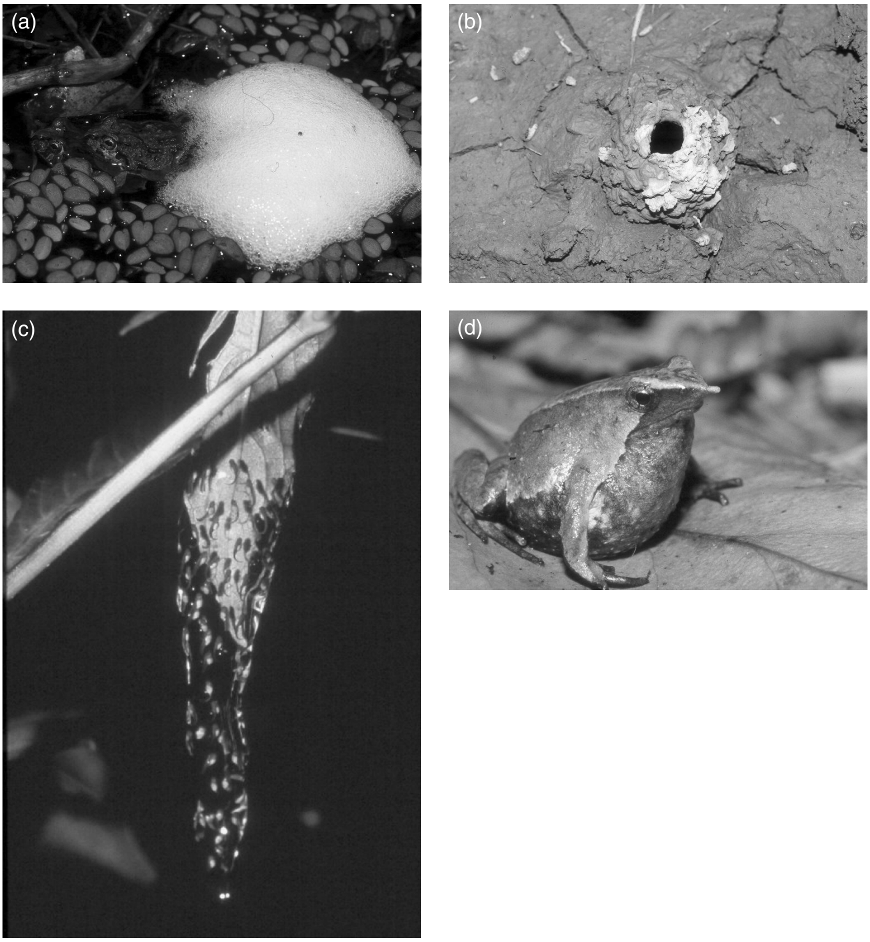

Fig. 1.2 Representatives of four anuran modes of reproduction. (a) *Pleurodema borelli* pair constructing a foam nest on the surface of water, from Argentina, (b) *Leptodactylus bufonius* mud nest by the edge of a depression, from Argentina, (c) *Hyla bokermanni* eggs on a leaf above water, from Ecuador, (d) male *Rhinoderma darwinii* brooding tadpoles in its vocal sac, from Chile. Photographs by Martha L. Crump.

Crinia georgiana from Australia oviposit in small water-filled depressions, seeps, or crevices on the ground where non-feeding larvae absorb their large yolks before metamorphosing.

Temperate and tropical frogs with terrestrial eggs and aquatic larvae accomplish this feat in diverse ways. Dendrobatids lay their eggs on land, but then a parent transports the larvae to water. In a few species of *Dendrobates*, the female also provides her young with unfertilized eggs as food. *Rhinoderma rufum*, from Chile, lays its eggs on land. The male takes late-stage eggs into his vocal sac where they hatch, then transports the larvae to water. In Europe, male midwife toads (*Alytes*) carry their eggs wrapped around their hind legs. Eventually they hop to ponds where the eggs hatch into aquatic larvae.

1.3.3.3 Arboreal/aquatic

Taxonomically diverse arboreal frogs lay their eggs on vegetation overhanging water. After the eggs hatch, the larvae fall into the water below where they continue to develop. *Agalychnis*, *Phyllomedusa*, and some *Hyla* from the New World tropics lay their eggs over standing water (Figure 1.2c), and neotropical centrolenids oviposit over flowing water. In some centrolenids, a parent protects the eggs from predators and keeps them moist by resting on them. Female *Afrixalus* from sub-Saharan Africa oviposit on leaves above water, then fold the leaf edges together and glue them in place with oviductal secretions. Some arboreal Old World rhacophorids and hyperoliids construct foam nests on vegetation overhanging temporary pools or slow-moving streams.

Water-filled basins offer oviposition sites that presumably lessen the risk of eggs getting swept away and reduce predation. Males of several neotropical gladiator frogs (e.g. *Hyla boans* and *Hyla rosenbergi*) construct basins beside streams or rivers. Water seeps in and fills the nests, and the frogs lay eggs as a surface film. After developing in the basin, the tadpoles metamorphose into froglets that take to the trees.

Some arboreal anurans oviposit in water-filled tree holes and axils of aerial plants. The eggs of many of these frogs (e.g. *Anodonthyla*, *Platypelis*, and *Plethodonthyla* from Madagascar) have large amounts of yolk. The tadpoles typically lack mouthparts, and they are non-feeding. In contrast, female *Osteopilus brunneus* from Jamaica lay eggs in water-filled leaf axils of bromeliads and continue to deposit about 250 more eggs in the bromeliad every few days throughout the tadpoles' development. The tadpoles—up to about 170 in a clutch—feed on the later-arriving eggs until they metamorphose into arboreal froglets.

Some arboreal frogs attach their eggs to the walls of water-filled cavities in trees. After hatching, the tadpoles drop into the water. In *Chirixalus eiffingeri*, an Asian rhacophorid, the female returns periodically and deposits fresh eggs for her tadpoles to eat. In others of this reproductive mode, the aquatic larvae feed on algae and debris.

In the New World tropics, female *Flectonotus* carry their eggs in dorsal pouches. After the eggs hatch as advanced tadpoles, the females transport them to water-filled bromeliads or bamboo where they complete development. Females of some neotropical *Gastrotheca* also brood their eggs in dorsal pouches and transport the tadpoles to aquatic sites.

1.3.3.4 Fossorial/aquatic

Scaphiopus and *Spea*, North American spadefoot toads, spend much of their lives underground but emerge following heavy rains and lay their eggs in newly formed ponds. The tadpoles develop quickly, which increases the probability of metamorphosing before the ponds dry. *Rhinophrynus dorsalis*, from southern Texas to Costa Rica, likewise lives underground and emerges after the first heavy rains to breed in temporary ponds. Female *Hemisis marmoratum* from Africa lay their eggs in subterranean chambers and stay with their eggs until after they hatch. At that point, the female digs a tunnel into adjacent water for the tadpoles.

1.3.3.5 Terrestrial/non-aquatic

Terrestrial anurans exhibit diverse life histories that free them from aquatic breeding sites. *Adenomera* from South America deposits foam nests under logs or in terrestrial cavities, and non-feeding tadpoles develop in the nests until they metamorphose. Neotropical *Eleutherodactylus*, *Oreophrynella* from Guyana and southern Venezuela, and New Guinean microhylids lay direct-developing eggs under logs or leaf litter. Many attend their eggs.

Some completely terrestrial anurans brood their young. Female *Assa darlingtoni* from Australia attend their terrestrial eggs. When the eggs are about 12 days old, the father climbs into the egg mass, rupturing the capsules. The newly hatched tadpoles wriggle into brood pouches, one along each side of the male's body. He broods his non-feeding larvae until they metamorphose into froglets. Female Darwin's frogs (*Rhinoderma darwinii*) from Chile and Argentina lay their eggs on moist ground. Just before the eggs hatch the males gobble them into their mouths and into the vocal sacs (Figure 1.2d). The young ingest secretions from the vocal-sac lining and emerge from their fathers' mouths as froglets.

Several *Nectophrynoides*, African bufonids, retain eggs in their oviducts and give birth to live young. In *Nectophrynoides occidentalis*, after depleting their yolk reserves the developing embryos feed on "uterine milk" secretion produced by glands in the mother's oviduct walls. These frogs live at high elevations, exposed to long periods of cold and drought. The females have a 9-month gestation period during which they estivate underground.

1.3.3.6 Arboreal/non-aquatic

Some neotropical *Eleutherodactylus* lay their direct-developing eggs in tree holes, bromeliads, moss, or on leaves. Some attend their eggs, others do not. *Eleutherodactylus jasperi* from Puerto Rico lived in arboreal bromeliads and gave birth to live young. The direct-developing eggs were retained in the oviducts, and nutrition came entirely from the embryo's yolk reserves. This species has not been seen since 1981 and is assumed extinct.

Female *Cryptobatrachus*, *Stefania*, and *Hemiphractus*, neotropical hylids, carry their direct-developing eggs exposed on their backs, secured by mucous gland secretions. Females of some *Gastrotheca* brood direct-developing eggs in dorsal pouches that protect the developing embryos from predators and desiccation and also function in gaseous exchange between the females and their embryos.

1.3.3.7 Fossorial/non-aquatic

The burrowing microhylid *Synapturanus salseri* from Colombia lays its eggs in burrows just below the root mat on the forest floor. Non-feeding tadpoles hatch at an advanced stage and absorb their yolk reserves. The Brazilian burrowing leptodactylid *Cycloramphus stejnegeri* likewise oviposits in underground nests and has non-feeding tadpoles. Other fossorial anurans, such as *Geocrinia* and *Arenophryne* (Australian myobatrachids), *Callulops* (New Guinean microhylids), and *Breviceps* (African microhylids), lay direct-developing eggs in underground burrows. Female *Breviceps* stay with their eggs and presumably keep them moist.

1.4 Amphibian declines and why they matter

The world is experiencing a "biodiversity crisis": rapid and accelerating loss of species and habitat (Ehrlich and Ehrlich 1981; Myers 1990; Raven 1990; Wilson 1992). Amphibians are part of this overall loss. Populations of amphibians are declining and disappearing worldwide at an increasing rate as compared to pre-1980 decades, even from protected areas (Blaustein and Wake 1990; Phillips 1994; Stuart *et al.* 2004). During the late 1980s and early 1990s, many declines seemed mysterious because there was no obvious cause. Skeptics argued that declines might be simply natural population fluctuations. Since the late 1980s, scientists worldwide have focused on determining the extent of declines and identifying the causes. We now know these declines are real.

The International Union for the Conservation of Nature (IUCN) assesses the status of species on a global scale and maintains and updates a catalog of taxa that face a high risk of global extinction: the IUCN *Red List of Threatened Species*. The 2008 update lists 30% of described amphibians as threatened with extinction (IUCN 2008). Since 1500, at least 39 species of amphibians have become extinct.

Scientists have hypothesized six major threats to amphibians: habitat modification and destruction, commercial over-exploitation, introduced species, environmental contaminants, global climate change, and emerging infectious diseases, especially the chytrid fungus *Batrachochytrium dendrobatidis* (Collins and Storfer 2003). Most agree the primary threat is habitat modification and destruction. For the past 100 years, human population growth has been exponential and has occurred largely in areas with the highest amphibian species richness: the tropics and subtropics (Gallant *et al.* 2007). As a result, these landscapes are being heavily modified to support agriculture and other human activities. The chytrid fungus also is exerting a major impact in many areas and on many species (Smith *et al.* 2006). Thus far the chytrid has caused the decline or extinction of about 200 species of frog (Skerratt *et al.* 2007). Many factors make the chytrid a significant concern, including its wide distribution in both the New and Old Worlds, its rapid spread and high virulence, and the fact that it infects a broad diversity of host species (Daszak *et al.* 1999).

Why should we care if we lose amphibians? It is for the same basic reasons we should care if other animals and plants disappear: economics, ecosystem function, esthetics, and ethics (Noss and Cooperrider 1994; Groom *et al.* 2006).

1.4.1 Economics

Selfishly, we should care if we lose amphibians because we use them for our own benefit, including for food and as pets. We use literally tonnes of frogs each year in medical research and teaching. We have isolated novel chemical compounds from granular glands of anuran skin and have used these compounds to develop new drugs.

1.4.2 Ecosystem function

Amphibians play a key role in energy flow and nutrient cycling because they serve as both predator and prey. By eating huge quantities of algae, tadpoles reduce the rate of natural eutrophication, the over-enrichment of water with nutrients, which leads to excessive algal growth and oxygen depletion. Most adult amphibians eat insects and other arthropods. As ectotherms, amphibians are efficient at converting food into growth and reproduction. Unlike endothermic birds and mammals that generate heat metabolically, amphibians expend relatively little energy to maintain themselves. Birds and mammals use up to 98% of their ingested energy to maintain their body temperatures, leaving as little as 2% to be converted to new animal tissue: food for predators. In contrast, amphibians convert about 50% of their energy gained from food into new tissue, which is transferred to the next level in the food chain

(Pough *et al.* 2004). If amphibians disappeared, would the world be overrun with houseflies, mosquitoes, and crop-eating insect pests? Would their predators go extinct?

1.4.3 Esthetics

Imagine the silence of rainy spring evenings without the lively croaking of male frogs. The monotonous roads without spring migrations of salamanders. People worldwide consider frogs to be good luck because of their association with rain. Amphibians provide inspiration for our artistic endeavors, from literature to music and the visual arts.

1.4.4 Ethics

Every species is a unique product of evolution. In 1982 the United Nations General Assembly adopted the World Charter for Nature, which states: "Every form of life is unique, warranting respect regardless of its worth to man, and, to accord other organisms such recognition, man must be guided by a moral code of action" (Noss and Cooperrider 1994). More than 100 nations signed the charter. Like all other living species, amphibians have intrinsic value and a right to exist.

Amphibians, amazing descendants of terrestrial pioneers, are fighting for their lives in a world greatly modified by humans.

1.5 References

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