

Amphibian Biology and Husbandry

F. Harvey Pough

Abstract

Extant amphibians comprise three lineages—salamanders (Urodela or Caudata), frogs and toads (Anura), and caecilians (Gymnophiona, Apoda, or Caecilia)—which contain more than 6000 species. Fewer than a dozen species of amphibians are commonly maintained in laboratory colonies, and the husbandry requirements for the vast majority of amphibians are poorly known. For these species, a review of basic characteristics of amphibian biology supplemented by inferences drawn from the morphological and physiological characteristics of the species in question provides a basis for decisions about housing and feeding. Amphibians are ectotherms, and their skin is permeable to water, ions, and respiratory gases. Most species are secretive and, in many cases, nocturnal. The essential characteristics of their environment include appropriate levels of humidity, temperature, and lighting as well as retreat sites. Terrestrial and arboreal species require moist substrates, water dishes, and high relative humidity. Because temperature requirements for most species are poorly known, it is advisable to use a temperature mosaic that will allow an animal to find an appropriate temperature within its cage. Photoperiod may affect physiology and behavior (especially reproduction and hibernation), and although the importance of ultraviolet light for calcium metabolism by amphibians is not yet known, ecological observations suggest that it might be important for some species of frogs. Some amphibians are territorial, and some use olfactory cues to mark their territory and to recognize other individuals of their species. All amphibians are carnivorous as adults, and the feeding response of many species is elicited by the movement of prey. Diets should include a mixture of prey species, and it may be advisable to load prey with vitamins and minerals.

Key Words: amphibian; caecilian; care; frog; herpetoculture; husbandry; salamander; toad

Introduction

Amphibians have a long history of service as research animals, especially as models for studies of embryonic development, regeneration, and physiological function. Salamanders (especially ambystomatids and salamandrids) and frogs (notably ranids and *Xenopus*) have contributed much to these studies, and methods for maintaining them in the laboratory are well established (Nace et al. 1974, O'Rourke 2002). Reviews of techniques for maintaining, breeding, and rearing these species of amphibians in captivity appear elsewhere in this *ILAR Journal* issue (Browne and Zippel 2007; Browne et al. 2007; O'Rourke 2007). Discussions of the requirements of some amphibians that are less commonly kept in captivity include the following: Buchanan and Jaeger (1995), Cover et al. (1994), de Vosjoli (1999), Johnson (1994), Maruska (1994), Pough (1991), Wake (1994), Zimmermann (1986), and Zimmermann and Zimmermann (1994).

Increased interest in organismal biology and in environmental and evolutionary physiology has brought novel species into the laboratory. These species often are selected for study because they have particular ecological, environmental, or phylogenetic characteristics. Because investigators and others have usually collected the animals from the wild, the individual animals have no history of exposure to captivity, and as species, they have not experienced selection for tolerance of captivity.

Currently there are no established husbandry methods for most species of amphibians, and only scanty information is available about ecology and behavior for many of them. Meeting the basic physical needs of a species—terrestrial or aquatic conditions, and the appropriate temperature and humidity—is obviously important, but other issues may be equally significant. Stimuli that elicit behavioral responses, for example, may inadvertently increase stress. The social behavior of amphibians is substantially more complex and subtle than one would guess from observations of laboratory colonies of *Xenopus* and axolotls (*Ambystoma mexicanum* and *Ambystoma tigrinum*). Social behaviors such as territoriality and dominance hierarchies may influence feeding and reproduction (e.g., Gabor and Jaeger 1995, Jaeger and Schwarz 1991, Jaeger et al. 1995, Murray and Jenkins 1999, Simons et al. 1997). Olfactory stimuli deposited on the substrate or carried through the air are elements of the behavioral ecology of some species of salamanders (Jaeger 1986). Lighting conditions may also be more important than we

F. Harvey Pough, Ph.D., is Professor of Organismal Biology, Department of Biological Sciences, Rochester Institute of Technology, Rochester, NY.

Address correspondence and reprint requests to Dr. F. Harvey Pough, Department of Biological Sciences, Rochester Institute of Technology, 85 Lomb Memorial Drive, Rochester, NY 14623, or email fhpsbi@rit.edu.

realize—photoperiod as well as the intensity and spectral quality of light are probably important stimuli for some amphibians.

Caring for exotic species of amphibians has much in common with herpetoculture, and herpetocultural resources can be useful sources of information and advice. Recommended resources include the Herpetocultural Library (de Vosjoli 2004, 2006; de Vosjoli et al. 2005); web sites (e.g., www.pumilio.com); and chat groups (e.g., www.groups.msn.com/HerpetocultureChatGroup/amphibians.msnw). In addition, information about the ecology, geographic ranges, and conservation status of amphibians is available from Amphibiaweb (www.amphibiaweb.org) and Global Amphibian Assessment (www.globalamphibians.org).

Herpetological Review, which the Society for the Study of Amphibians and Reptiles publishes, includes a section on Herpetological Husbandry; and the International Zoo Yearbook includes information about the care of amphibians. Professional staff members at zoos and aquaria may be able to provide suggestions about the husbandry of particular species.

When species-specific information about the behavioral, ecological, and physiological characteristics of a species of amphibian is not available, inferences based on elements of the basic biology of amphibians may provide the only guidelines. Two characteristics of amphibians—ectothermal regulation of body temperature and permeable skin—play central roles in their biology and provide starting points for inferences about their requirements in captivity. It is possible to amplify these general characteristics with information about the phylogenetic relationships and by observations of the morphological characteristics of the species in question.

Biological Characteristics and Life Style of Amphibians

The extant amphibians (Amphibia [Frost 2006] or Lissamphibia [Tree of Life Web Project 1995]) appear in the fossil record during the Mesozoic. A large number of derived characters (initially identified by Parsons and Williams [1963] and subsequently restated and modified [Duellman and Trueb 1985, Frost 2006]) support the monophyly of the group. The lower Triassic form *Triadobatrachus* forms a monophyletic group with frogs and toads (Rage and Roček 1989). The earliest salamander fossils are from Middle Jurassic sites in England and Kirghizstan, and investigators have recently reported superbly preserved fossil salamanders from the Late Jurassic of China (Evans et al. 1988; Gao and Shubin 2001, 2003; Gao et al. 1998; Nesson 1988). The earliest known caecilian, *Eocaecilia*, is from the Early Jurassic of Arizona (Jenkins and Walsh 1993). Thus, the morphological and physiological characteristics of the major lineages of amphibians have been established for 150 million years or more. These characteristics are central to the evolutionary persistence of the lineages and are key elements of the biology and husbandry of amphibians.

Phylogenetic and Ecological Diversity

A recent revision of the extant amphibians (Frost 2006) has resulted in a change of the generic names of many species. The literature of amphibian biology uses the old names, and literature searches require these names. To minimize confusion, I have used the familiar names with the new names in parentheses.

The extant amphibians illustrate an approach to terrestrial vertebrate life that combines ectothermy and a low metabolic rate with highly efficient secondary production (Pough 1983). A low metabolic rate reduces the mass-specific metabolic rate with the result that small body size is energetically feasible. Most amphibians are small. Twenty percent of the species of salamanders and 17% of frog species have adult body masses of 1 g or less, and 65% of salamanders and 50% of anurans are smaller than 5 g as adults. Because they are ectotherms, amphibians do not use ingested energy to control their body temperature. As a result, their net secondary production efficiency is high—amphibians convert half or more of the energy they ingest into their own body mass compared with less than 1% for birds and mammals. The combination of small body size and efficient biomass production allows amphibians to play a unique role in ecosystems by consuming prey items that are too small for other vertebrates to eat and by repackaging most of that energy into salamander and frog-size packages (Pough 1980).

The skin of amphibians lacks scales, is plentifully supplied with mucus and poison glands, and is a site of oxygen and carbon dioxide exchange for adults as well as for larvae. Small body size and glandular skin profoundly influence the ecology, physiology, and behavior of amphibians. Cutaneous respiration accounts for a significant proportion of respiratory gas exchange, water evaporates from the skin of some amphibians as rapidly as from a free-water surface, and amphibians are sensitive to toxins in the environment (Alford and Richards 1999; Boutilier et al. 1992; Maerz et al. 2005; Shoemaker et al. 1992).

The discussion that follows emphasizes features that are helpful starting points for inferences about the habits, habitats, and husbandry of unfamiliar species of amphibians.

Frogs and Toads

Anurans are the largest group of amphibians. Approximately 5200 species are in this group (Frost 2006), and they reside on all of the major continents except Antarctica and on many oceanic islands (Pough et al. 2004; Zug et al. 2001). Compared with other tetrapods, anurans have short trunks (only 5–9 presacral vertebrae), broad, flat heads with extensive reduction of bone, and hind limbs that are substantially longer than the forelimbs in most species. Although the long hind limbs of anurans are most commonly associated with jumping, they are also effective for swimming, walking, running, and climbing; and all of these forms of locomotion are represented among frogs and toads.

Common names do not match the phylogenetic or ecological diversity of the extant anurans and are not a good guide to their habits or husbandry. Some animals with frog in their names are fully aquatic (e.g., the African clawed frogs, *Xenopus*), but others are semiaquatic (e.g., many species of true frogs, Ranidae) or fully terrestrial (e.g., the dart-poison frogs, Dendrobatidae). Animals called toads are often more terrestrial than those called frogs, but exceptions (e.g., the completely aquatic Surinam toad [*Pipa pipa*]) make that distinction an unreliable guide for husbandry. An animal called a tree frog is almost certainly at least partly arboreal, but many frogs and toads without “tree” in their common names have substantial arboreal capacities and are best maintained in cages that permit them to climb, absorb water droplets from leaves, and hide in foliage.

Body form is likely to be a more reliable guide to the habits and needs of an unfamiliar species of anuran than its name, and some generalizations about form and ecology are robust (Figure 1). Arboreal species of frogs normally have long limbs. Familiar examples are found in the hylids (tree frogs that are most diverse in the New World and occur also in Europe, parts of Southeast Asia, and Australia) and their ecological counterparts the rhacophorids (tropical Africa, parts of Asia, and the Indo-Australian archipelago), as well as in less familiar groups such as hyperoliids (sub-Saharan Africa, Madagascar, and the Seychelles) and centrolenids (Central and South America). Some lineages of arboreal frogs have expanded toe pads that help them adhere to smooth surfaces. The bottom surface of a toe pad is formed

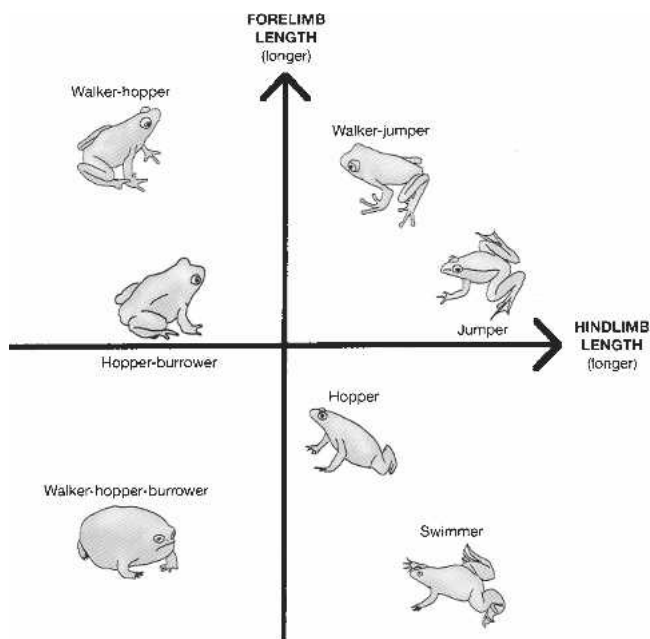


Figure 1 Relationship between body form and locomotor mode among anurans. Reprinted with permission from Pough FH, Janis CM, Heiser JB. 2005. *Vertebrate Life*. 7th ed. Saddle River: Prentice Hall.

by polygonal columnar epithelial cells that are separated by crevices (Green 1979). Glands secrete a watery fluid that promotes capillary adhesion between the flat surfaces of the epithelial cells and the substrate. The adhesive force that is produced is strong enough to allow small species of frogs to climb smooth vertical surfaces, including the glass walls of terraria, and to adhere to the underside of a leaf or a glass terrarium cover (Green 1981).

Stout bodies and blunt heads are often characteristic of terrestrial anurans, and species that normally move by walking or running usually have relatively short legs and forelimbs and hind limbs that do not differ greatly in length. Many species of toads (Bufonidae, a nearly worldwide group) have stout bodies and blunt heads with relatively short legs, as do terrestrial frogs (Leptodactylidae, primarily a Central and South American group, and Microhylidae, from southern North America to northern South America, sub-Saharan Africa, Southeast Asia and eastern China, and islands of the western Pacific Ocean). Anurans that burrow into the ground generally have stout bodies and short limbs that place them at the extreme end of the terrestrial walkers, and some burrowers have pointed snouts and tarsal features (e.g., the cornified spade of spadefoots) that assist in burrowing.

Salamanders

The approximately 550 species of salamanders are elongate animals with long tails. The forelimbs and hind limbs of terrestrial salamanders are roughly the same length, and salamanders use alternating movements of the limbs combined with the passage of a sine wave along the body axis for locomotion. Some fully aquatic species of salamanders have reduced limbs. Salamanders have a more restricted geographic distribution than do anurans. They are largely absent from the Southern Hemisphere, extending southward only as far as the northern half of South America and the north coast of Africa (Pough et al. 2004; Zug et al. 2001). Approximately 70% of extant salamanders are in the family Plethodontidae. This family is well represented in North, Central, and South America and has a single species in southern Europe and another in Korea.

Salamanders exhibit less obvious morphological diversity and habitat specialization than do anurans although salamanders reside in a variety of habitats, from aquatic to terrestrial. Plethodontids extend from arboreal through terrestrial to aquatic species, with few conspicuous differences in body form. Most plethodontids (hence, most salamanders) dwell in streams, on stream banks, or on the forest floor, but some tropical plethodontids are arboreal. Arboreal salamanders have webbed feet that adhere to smooth surfaces as the salamanders climb. Salamanders without specialized feet also climb; *Plethodon cinereus* climb on plants in the forest understory to forage on wet nights (Jaeger 1978). Streamside plethodontid salamanders extend from species that normally live on the edge of a stream or in the water (e.g., *Eurycea* and *Gyrinophilus*), through a series of

increasingly terrestrial species of streamside salamanders (*Desmognathus*) that occur in habitats progressively farther from water, to fully terrestrial species in the genus *Plethodon*, which never enter water (Hairston 1987).

Salamandrids also span a range from aquatic to terrestrial. Aquatic salamandrids—the European *Triturus* (*Lisso-triton*) and the North American *Notophthalmus*—have few features that reveal their aquatic habits except for tails that are laterally compressed compared with the more rounded tails of terrestrial forms such as *Salamandra* in Europe and *Taricha* in North America.

Some terrestrial species of salamanders (e.g., *Ambystoma* and *Taricha*) breed in water. These species develop aquatic characteristics such as an expanded tail fin during the breeding season. Fully aquatic species of salamanders often have paedomorphic characteristics that include externally visible features such as the absence of eyelids and retention of a functional lateral line system. External gills are the most conspicuous feature of some aquatic species such as the mud puppies (*Necturus*). However, not all aquatic salamanders have external gills. The largest extant salamanders—the Chinese and Japanese giant salamanders (*Andrias*), which reach adult lengths of 1.5 m or more, and the North American hellbenders (*Cryptobranchus*), which grow to 75 cm—are aquatic but lack external gills. An eel-like body form with extreme reduction in the size of the limbs is characteristic of two families of aquatic salamanders, the sirens (*Siren* and *Pseudobranchus*) and the amphiumids (*Amphiuma*).

Facultative or obligatory paedomorphosis occurs among some species of ambystomatids. In some species, entire populations retain external gills and other larval characteristics and pass their entire lives in water (Whiteman 1994). The familiar laboratory axolotls are an example of this phenomenon. In other species, individuals within a population are paedomorphic. The incidence of paedomorphosis varies geographically in *Ambystoma tigrinum* (Collins 1981) and from pond to pond in *Ambystoma talpoideum* (Semlitsch 1985). Paedomorphosis also occurs in some other families of salamanders, including salamandrids (*Notophthalmus*) and dicamptodontids (*Dicamptodon*) (Good 1989; Harris 1987).

Caecilians

The Gymnophiona is a lineage of elongate, limbless, and nearly tail-less amphibians known as caecilians, which includes both terrestrial burrowing species and aquatic species (Taylor 1968, Wilkinson and Nussbaum 2007). The approximately 170 species live in tropical areas of most of the world, but the group is absent from Madagascar and the Papuan-Australian region. Their secretive habits make caecilians difficult to study, but new techniques are revealing important information about the ecology of this group (Gower and Wilkinson 2005; Gower et al. 2004; Kupfer et al. 2006a; Measey et al. 2003a, 2003b, 2004; Preswell et al. 2002).

The most important decision about the husbandry of a caecilian is whether to keep it in an aquarium or a terrarium, and that question is not always easy to answer. Aquatic and terrestrial species of caecilians are not always distinguished by conspicuous morphological differences. The eyes of all species are greatly reduced and covered by skin, and all caecilians have a unique chemosensory organ—the tentacle—that incorporates elements of the eye and the vomeronasal organ. Aquatic species are somewhat laterally flattened, and some of them have colored patterns on their skin. These characteristics contrast with the cylindrical body form of terrestrial species and the uniform surface coloring of most of those species.

Life History

A complex life history that includes an aquatic larval stage and metamorphosis to the adult form is an ancestral characteristic of amphibians, but enormous interspecific variation exists even within this pattern. Only fishes have more diverse life history patterns than amphibians. The diversity of life history strategies in amphibians complicates generalizations about animal husbandry. Direct development (omitting a free-living larval stage) and viviparity (retaining the eggs within the female through metamorphosis) occur in all groups of extant amphibians.

Salamander larvae are similar to adults in general body form although they lack some characteristics such as eyelids and certain jaw bones, which appear only at metamorphosis. Salamander larvae are carnivorous, as are all adult salamanders. The most visible change that accompanies metamorphosis of salamanders is loss of the gills and tail fin. Direct development, which is widespread among plethodontid salamanders, occurs also in *Ambystoma* and *Salamandra*. The eggs of direct developing species are permeable and require high humidity levels to avoid desiccation.

Frog larvae (tadpoles), in contrast to salamander larvae, are very different from the adults in body form and function. It is only a mild exaggeration to say that a tadpole is a feeding machine with just enough locomotor capacity to move it from one food source to the next. Tadpoles are filter feeders, and they remove particles of food from the stream of water that passes inward through the mouth and out past the gills. Grazers, predatory forms, and egg-eaters use cornified beaks to loosen particles from a large surface, and midwater feeders sieve particles that are already suspended in water. Papillae in the buccal cavity direct large suspended particles to the esophagus, and mucus captures smaller particles. Strands of mucus and captured particles break loose and are carried to the esophagus. Algae and bacteria comprise the diet of most tadpoles, but some species are macrophagous, consuming zooplankton and small crustaceans. Carnivorous tadpoles prey on other tadpoles (of their own species or other species), and egg-eating tadpoles consume eggs. Oophagous tadpoles live in small bodies of water known as phytotelmata, such as in the leaf axils of plants.

Some consume eggs that are incautiously deposited by a female (of their own species or a different species) in an axil that already contains a tadpole. Dendrobatid frogs deposit eggs in terrestrial nests, and one parent remains with the clutch until the eggs hatch into tadpoles that are transported to aquatic sites. Female *Dendrobates (Oophaga) pumilio* transport tadpoles to phytotelmata and place one tadpole in each site. The mother returns to her tadpoles and deposits nutritive eggs during the developmental period (Brust 1993).

Some caecilians deposit large-yolked eggs on land. These eggs hatch into free-living aquatic larvae that spend approximately 1 year in the water before they metamorphose to become terrestrial adults. Viviparity is widespread among caecilians; all species in the subfamilies Typhlonectinae and Scolecomorphinae are believed to be viviparous. The subfamily Caeciliinae includes viviparous species, species that lay eggs which hatch into aquatic larvae, and species that lay eggs with direct development (Wake 1977, 1993). Viviparous caecilians produce small-yolked eggs that hatch into larvae within the mother's oviducts. When the energy supplied by the yolk has been consumed, the larvae of viviparous caecilians feed on a lipid-rich material secreted by the walls of the oviduct or by the skin (Kupfer et al. 2006b; Wake 1993; Wake and Dickie 1998).

Viviparity appears to be rare among salamanders and frogs, yet it has evolved repeatedly in both groups (Wake 1993). *Salamandra atra* gives birth to fully metamorphosed young, and other species of salamandrids retain the eggs through hatching and produce aquatic larvae. Viviparity in the strict sense of retaining eggs in the oviducts through the entire developmental period is currently known in only two genera of anurans—a Puerto Rican tree frog, *Eleutherodactylus jasperi*, and a genus of African toads, *Nectophrynoides*, which includes species that span the entire range from external fertilization and aquatic tadpoles to internal fertilization and viviparity (Graybeal and Cannatella 1995; Wake 1978). Viviparity is easy to overlook in the field, however, and it is probably more widespread among anurans than we currently realize.

Ectothermy and Temperature Regulation

In general, amphibians are regarded as poor thermoregulators compared with other terrestrial vertebrates (Brattstrom 1962, 1963, 1979; Hutchison and Dupré 1992). Some habits and habitats offer limited opportunities for thermoregulation, at least during the portion of the day when the animals are active. Nocturnal species, for example, cannot bask in the sun, and the thermal mosaic of the environment is more uniform at night than it is during the day. Furthermore, evaporative cooling counteracts solar heating, and water loss limits the time most species of amphibians can be in exposed locations (Tracy 1975).

Amphibians' thermoregulation under natural conditions

is probably more common than we appreciate, however, because much of their thermoregulatory behavior consists of selecting suitable microenvironments. Newly metamorphosed spotted salamanders, *Ambystoma maculatum*, for example, take shelter beneath rocks on the banks of their breeding ponds. The salamanders select sites under rocks that do not exceed 32°C during the day. In laboratory trials in which rocks were heated, salamanders emerged and sought cooler shelters when the temperature beneath a rock reached 32°C (Pough and Wilson 1970). Red efts, the terrestrial life stage of red-spotted salamanders (*Notophthalmus viridescens*), take shelter beneath pieces of bark in a forest clearing. They tolerated body temperatures between 26 and 29°C although lower temperatures were available under the same piece of bark; however, an investigation revealed no salamanders under bark slabs when temperatures exceeded 30°C (Pough 1974).

The permeable skin of amphibians both complicates their thermoregulatory behavior and provides opportunities that would not be available to animals with lower rates of cutaneous water loss. Pearson and Bradford's (1976) comparison of a toad (*Bufo [Chanus] spinulosus*) and a lizard (*Liolaemus multiformis*) in the high Andes illustrates the limits that the permeable skin of amphibians places on their ability to increase their body temperatures by basking in the sun. Both animals basked in the sun and increased their body temperatures above air temperature. Although the lizard reached body temperatures between 30 and 35°C, the toad's body temperature did not exceed 25°C because of the cooling effect of cutaneous evaporation. Newly metamorphosed green toads, *Bufo (Anaxyrus) debilis*, bask in the sun on the sides of streams but seek areas of moist substrate to avoid dehydration (Seymour 1972). Adult bullfrogs, *Rana catesbiana (Lithobates catesbeianus)*, spend the night in artificial ponds in California that remain warmer than the air, and the animals move onto shore during the day (Lillywhite 1970). Frogs that are partly submerged are able to remain in full sun for prolonged periods because evaporative water loss balances solar heating and allows them to maintain body temperatures between 25 and 30°C whereas black bulb temperatures exceed 40°C. Canyon treefrogs (*Hyla arenicolor*) in Arizona spend the day in full sun on boulders near streams. Apparently cutaneous evaporation prevents the frogs from overheating, but the investigators observed that they did become dehydrated. At intervals the frogs shuttled to the stream to rehydrate and then returned to a boulder (Brust and Preest 1988). Avoidance of predation by garter snakes (*Thamnophis*) is a plausible explanation for this behavior because the snakes forage along the water's edge but cannot cross the hot boulders to reach the frogs.

Temperature and Husbandry

Amphibian husbandry requires information about the temperatures at which animals should be maintained, but it is not possible to provide specific recommendations for am-

phibians in captivity. Although the temperature relations of amphibians are flexible, their temperature preferences and temperature tolerance may change daily or seasonally in response to the recent thermal history of the animals, to social interactions, or with age (summarized in Hutchison and Dupré 1992).

The nocturnal habits of most amphibians and the interaction of heat loss (via evaporative cooling) with heat gain (via radiation and conduction) preclude generalizations about temperature regulation. Free-ranging animals probably use microclimate selection to adjust their body temperatures, and they may regulate for only a portion of the day. Species that are active at night, for example, probably must choose between being active at whatever body temperature results from the ambient conditions or forgoing activity for that evening. These species may thermoregulate during the day, however, by moving within their retreat sites as some nocturnal lizards do (Mautz and Case 1974). Aquatic larvae and the adults of fully aquatic species normally have body temperatures that are very close to water temperature; however, under natural conditions tadpoles select different locations during the day in response to temperature changes (Brattstrom 1962).

Temperatures recorded in the field reflect the ranges of temperatures that amphibians have tolerated and provide a starting point for husbandry. Based on the temperatures that Duellman and Trueb (1985) and Hutchison and Dupré (1992) have tabulated, it is advisable to use the following guidelines when housing amphibians:

- For species that live only in cold aquatic habitats (e.g., *Ascaphus*, *Cryptobranchus*, *Necturus*, *Gyrinophilus*), initially set the temperature at 10°C.
- For species from cool temperate and montane tropical regions, start with temperatures around 15°C.
- For species from warm temperate and tropical environments, evaluate the responses of the animals to temperatures between 20 and 25°C.

These estimates are intentionally on the cool side because a temperature that is too high is more dangerous than one that is too low.

Many species of amphibians are kept by herpetoculturists. Specific information about these species is available on the web and includes the following suggestions:

- www.pumilio.com suggests a temperature of $\geq 18^\circ\text{C}$ for dart poison frogs (Dendrobatidae);
- www.goecities.com/rafardell/husbandry.html suggests temperatures between 26 and 30°C for adult *Ceratophrys*; and
- www.peteducation.com recommends 18 to 24°C for *Bombina*.

Web sites are likely to be particularly useful sources of information about exotic species, which are not typically

included in publications that focus on the species commonly used in laboratories.

Observation of the animals' color and behavior (activity, feeding, and production of feces) provides a basis for adjusting temperature. If animals are dark-colored, inactive, do not feed, or do not produce feces, it is advisable to increase the temperature in small increments. Ideally, captive conditions will replicate the thermal mosaic found in natural habitats and will allow animals to maintain daily cycles of temperature and behavior. However, providing both high humidity and a temperature mosaic simultaneously requires care to avoid creating a steamer that risks overheating the animals it is intended to benefit. One suggestion is to place an under-cage heater at one end of a long terrarium to establish a temperature gradient that may allow amphibians to thermoregulate behaviorally. Under-cage heaters are widely available from herpetocultural suppliers.

Water Uptake and Loss

Evaporation is the major route of water loss for terrestrial amphibians (Shoemaker et al. 1992). Some species have very low cutaneous resistances, but others have substantially less permeable skins. Investigators have characterized anurans according to the following three general categories of skin resistance to water movement (Buttemer 1990; Shoemaker et al. 1972, 1989; Wygoda 1984, 1988):

- Skin resistance < 1 sec/cm of skin thickness: Many aquatic and terrestrial species (including species of spadefoot toads [*Scaphiopus*]), which live in deserts)
- Skin resistance of 2 to 10 sec/cm: Arboreal species
- Skin resistance of 100-300 sec/cm: A few species of tree frogs, which are relatively waterproof

This pattern of skin resistance appears to include both phylogenetic and ecological components. All of the species with a high level of cutaneous resistance are found among hylids, rhacophorids, and hyperoliids, but arboreal species of North American hylids have higher levels of cutaneous resistances than do nonarboreal species (Wygoda 1984).

Waterproof species have mechanisms that reduce water movement through the skin. *Phyllomedusa sauvagii* uses its limbs to spread a waxy secretion from glands over its body. Lipids in the skin are probably the basis of the high levels of cutaneous resistance of *Chiromantis*, *Hyperolius*, *Litoria*, and *Hyla* (Barbeau and Lillywhite 2005; Christian et al. 1988; Shoemaker et al. 1992).

The permeable skins of amphibians allow water to move inward as well as outward, and amphibians rely on cutaneous uptake of water rather than on drinking. The pelvic patch is an area of highly vascularized skin responsible for most cutaneous water uptake. Water is absorbed by skin in the pelvic patch from pools or droplets, and also from moist soil. The relationship between soil water content and water uptake is complex and depends on the structure of the soil

and the surface texture of the skin. Rugosity typically characterizes the skin of the pelvic patch of terrestrial amphibians, especially those from relatively dry environments, and these species can generally absorb water from lower soil water potentials better than can aquatic species.

The matrix water potential level of soil must be relatively high to permit absorption of water by amphibians. A frog (*Rana [Lithobates] pipiens*) that has been dehydrated to 70% of its fully hydrated body mass has a water potential of -400 kPa (Tracy 1976). Water potentials in the range of -100 to -200 kPa allow water uptake by normally hydrated amphibians. (For horticultural potting soil, this water potential corresponds to soil that can be squeezed into a ball that does not crumble when the pressure is removed.)

Photoperiod and Light Quality

The light cycles in animal rooms that house amphibians should accommodate the needs of the resident species, although day and night (photophase and scotophase) can be shifted for the convenience of the investigator. It is important to note that because even nocturnal species need light to detect prey, the night phase of a photoperiod cycle should include low-intensity light.

Photoperiod, perhaps perceived by extraocular pathways, influences reproductive cycles of amphibians as it does for other vertebrates. Photoperiod is also involved in the timing of metamorphosis (Campbell et al. 2001; Paniagua et al. 1990; Wright 2002); however, we do not yet know about the effects of different spectral distributions of energy on these functions.

Exposure to ultraviolet-B light (UV-B¹) is an essential element of husbandry for some species of lizards (e.g., Gehrmann et al. 1991; Townsend 1979; Townsend and Cole 1985), whereas other species appear to thrive without ultraviolet light. The role of UV-B in amphibian physiology is less clear (Gehrmann 1994). Studies of the effect of ultraviolet light on amphibians have emphasized its deleterious effects on eggs and embryos (e.g., Blaustein and Belden 2003; Blaustein et al. 1997; Broomhall et al. 2000; but see also Licht and Grant 1997 for a contrasting opinion); however, the behavior of some species of frogs exposes them to direct solar radiation for hours at a time (Brust and Preest 1988; Lillywhite 1970; Seymour 1972). Fluorescent bulbs with high UV-B output had no apparent ill effects on the growth of juvenile Wyoming toads (*Bufo [Anaxyrus] baxteri*) (R.K. Browne, Perth Zoo, South Perth, Western Australia, personal communication, 2006), but larval salamanders (*Ambystoma macrodactylum* and *Ambystoma gracile*) that were exposed to UV-B grew more slowly than individuals that received only full-spectrum illumination (Belden and Blaustein 2002). Adults of two species of poi-

son dart frogs (Dendrobatidae) avoided sites with high UV-B flux in the field and chose low levels of UV-B illumination in cages (Han et al. 2007). This is an area in which further experiments are needed. Gehrmann (1987) has provided information about the spectral quality of light from a variety of lamps.

Chemical Ecology

A variety of noxious or toxic chemicals protect amphibians and include the following: alkaloids, peptides, biogenic amines, and bufodienolides (Brodie 1983; Daly 1995; Daly et al. 1987; Erspamer 1994). Some of these chemicals are derived from arthropods in the diets of the animals (Clark et al. 2005; Daly et al. 2000; Darst et al. 2005; Saporito et al. 2003, 2004; Weldon et al. 2006). Species with potent chemical defenses are often warningly colored, but this is not always the case. Toads (family Bufonidae) contain bufodienolides, which can be toxic to predators, but most toads are cryptically colored. Other species with noxious or toxic secretions have cryptic colors and patterns on the dorsal surface as well as bright flash colors on the ventral surface that are revealed by defensive displays. When fire-bellied toads (*Bombina*) are attacked, for example, they bend the trunk upward to display the red or yellow ventral surface. Similarly, fire-bellied newts (*Cynops*) and California newts (*Taricha*) expose brightly colored ventral surfaces on the trunk and tail when they are threatened. These defensive chemicals can be toxic to other species of amphibians, particularly when individuals are crowded together.

Chemical communication is widespread among plethodontid salamanders and may also occur in other terrestrial species. Red-backed salamanders (*Plethodon cinereus*) identify conspecific individuals by scent and respond differently to the scents of neighbors and strangers (Jaeger 1981; Jaeger and Forester 1993; Jaeger and Peterson 2002). It is important to recognize that moving animals among cages may be stressful because olfactory communication may cross species lines and the new cage may contain the scent of unfamiliar conspecifics. Smith and Pough (1994) have described intergeneric aggression of plethodontid salamanders.

Housing and Diet

Amphibians are secretive animals that spend substantial parts of the day in retreat sites. For this reason, the provision of hiding places for these animals is a basic element of successful husbandry. Amphibians are often reluctant to move into areas where they feel exposed, therefore some type of cage furnishing is an important component of housing. Naturalistic terraria with soil, plants, and pools of water are aesthetically pleasing, but it is difficult to keep such an enclosure clean and it is not clear whether amphibians appreciate them as much as human observers do.

¹Abbreviation used in this article: UV-B, ultraviolet-B light.

Anurans and salamanders often thrive in cages with moist paper as substrate, sections of plastic pipe as hiding places, and plastic aquarium plants as cover objects. This utilitarian housing is easier to clean than a naturalistic terrarium, which is an important consideration when large numbers of individuals are maintained. The use of inert materials for amphibians is important because of the permeability of their skin. For example, the sensitivity of amphibians to the acids and bleaches that are used to manufacture paper make laboratory filter paper a better choice than paper towels, and distilled, deionized, or spring water is preferable to chlorinated tap water.

Importance of Live Prey

Aquatic amphibians (e.g., tadpoles, salamander larvae, and adults of species such as *Xenopus* and axolotls) accept prepared diets, but terrestrial species often respond only to the stimuli provided by moving prey items. Most amphibians feed on insects, although the largest species consume crustaceans and small vertebrates. Bullfrogs (*Rana* [*Lithobates*] *clamitans*) and cane toads (*Bufo* [*Chanos*] *marinus*) are notorious for eating other species of anurans, and the horned toads of South America (*Ceratophrys*) lure smaller frogs within reach by wiggling a toe in a way that simulates the movements of an insect.

Frogs' eyes respond preferentially to small, convex, dark stimuli that move across the field of view. These neural circuits have been called bug detectors (Lettvin et al. 1959). Reliance on hard-wired prey detection mechanisms to elicit a feeding response may explain why anurans and salamanders do not respond to motionless prey. Moving an inanimate food item in front of an amphibian can stimulate attack; however, the size, shape, and pattern of movement of the item must fall within the range of stimuli to which bug detectors respond.

Despite the stereotypy of feeding responses that bug detector circuitry has implied, at least some amphibians change their response to prey under different circumstances. Undisturbed red-backed salamanders (*Plethodon cinereus*) selected large fruit flies when they were given a choice between large and small flies, and this behavior conforms to the predictions of optimal foraging theory (Jaeger 1990).

Nutritional Quality of Prey

Amphibians consume whole insects. Practical considerations usually limit the choice of food items to several species of invertebrates that are readily available commercially, which include the following: mealworms (*Tenebrio molitor*), gray crickets (*Acheta domesticus*), wax worms (*Galleria mellonella*), cockroaches (usually *Blaberus craniiferus*), wingless fruit flies (*Drosophila melanogaster*), and earthworms (*Lumbricus terrestris*). Insects are generally deficient in vitamins and have low calcium:phosphorus ratios

(Barker et al. 1998). None of these species (with the possible exception of earthworms) is suitable as the sole component of a diet (Bernard and Allen 1997).

It is possible to supply vitamins and minerals by mixing a bird or reptile multivitamin powder with powdered calcium or a commercial preparation of calcium with vitamin D₃ and dusting the insects with this mixture just before offering the food items to the amphibians (Allen and Oftedal 1989). Another way to improve the nutritional content of insects is to feed supplements to them—a process called gut-loading. Ground rodent chow, monkey chow, trout chow, tropical fish flakes, and high-protein baby cereal have been used for gut loading. In a comparative study, juvenile Wyoming toads (*Bufo* [*Chanos*] *baxteri*) fed crickets that had been gut-loaded with an experimental diet that included spirulina (high levels of vitamin A) and fish oil (high in omega-3 fatty acids) ate more and grew faster than toads that ate crickets dusted with powdered vitamins and minerals (R. K. Browne, personal communication, 2006).

Because powdered vitamins and minerals adhere to prey items for only a short time and nutrients in the gut are transient, it is important to remove uneaten food items within a few hours. In addition, because hungry insects may attack amphibians, it is wise to remove insects that are not eaten immediately as a precaution.

Summary

About a dozen species of amphibians are commonly maintained in captivity, and husbandry methods for those species are well established. Caring for individuals of any of the remaining 6000 or so species of frogs, salamanders, and caecilians requires integrating knowledge of the basic biological characteristics of amphibians with information about the behavior and ecology of the species in question. Herpetoculturists have developed methods for maintaining exotic species of amphibians, and herpetocultural publications and web sites may provide useful information. Frequently little information is available about a species, and in that situation, it is necessary to draw inferences from morphological characteristics of the species.

Ectothermy and a permeable skin are basic characteristics of amphibians. In captivity, terrestrial species require a source of heat for thermoregulation and a closed environment that maintains a high humidity within the cage. The combination of heat with a closed container creates a risk of lethal overheating, therefore cages should provide a thermal mosaic from which the animal can select conditions that match its preference.

Many amphibians are nocturnal, spending the day in hiding places and emerging at night to feed. Terrestrial amphibians locate prey by vision, and consequently animal rooms require a low level of illumination at night. The significance of ultraviolet light to amphibians is unclear. A substantial body of literature has documented harmful effects of ultraviolet radiation on amphibian eggs, and adults

of some species of tropical forest frogs avoid exposure to ultraviolet light. However, some species may require exposure to ultraviolet light for vitamin D activation and calcium metabolism.

Most amphibians feed in response to the movement of prey items, and live prey is usually necessary. Insects are the most common food for amphibians in captivity, but insects do not provide a nutritionally complete diet. Feeding a variety of insects is advisable, as is supplementing the insects with vitamins and minerals. Powdered vitamins and minerals can be dusted onto an insect just before it is fed to an amphibian, or high concentrations of these substances can be included in the food of the prey insects. Uneaten prey should be removed from the cage promptly because the nutritional supplements are quickly lost, and hungry insects may attack the amphibian.

Chemicals play a large role in the ecology and behavior of amphibians, and must be considered in husbandry. Many species of amphibians are protected by toxic secretions, and in some situations these substances can be lethal to other species. For this reason, it is unwise to carry different species in the same small container, and it may be unwise to mix species in cages. Salamanders, at least, have extensive social behaviors that are mediated by chemical cues from conspecifics. Some salamanders can recognize other individuals by scent, for example, and the scent of a strange salamander elicits behavioral responses different from those produced by the scent of a familiar individual. Observations of interspecific aggression suggest that chemical stimuli might cross species lines as well. It is essential to clean all of the equipment used to contain and handle amphibians after each use to remove scent cues.

Because amphibians differ in so many respects from their human caretakers, successful husbandry requires combining an appreciation of the biology of these animals with awareness of elements of the physical and biological environment that are insignificant or even imperceptible to humans and sensitivity to subtle changes in the colors, postures, and behaviors of the amphibians themselves.

Acknowledgments

Larry Buckley, John Cadle, Alan Savitzky, Ellen Smith, Stephen Smith, and two anonymous reviewers provided helpful advice and suggestions.

References

- Alford RA, Richards SJ. 1999. Global amphibian declines: A problem in applied ecology. *Ann Rev Ecol Syst* 30:133-165.
- Allen ME, Oftedal OT. 1989. Dietary manipulation of the calcium content of feed crickets. *J Zoo Wildl Med* 20:26-33.
- Barbeau TR, Lillywhite HB. 2005. Body wiping behaviors associated with cutaneous lipids in hylid tree frogs of Florida. *J Exp Biol* 208:2147-2156.
- Barker D, Fitzpatrick MP, Dierenfeld ES. 1998. Nutrient composition of selected whole invertebrates. *Zoo Biol* 17:123-134.
- Belden LK, Blaustein AR. 2002. UV-B induced skin darkening in larval salamanders does not prevent sublethal effects on growth. *Copeia* 2002: 748-754.
- Bernard JB, Allen ME. 1997. Feeding captive insectivorous animals: Nutritional aspects of insects as food. *Nutrition Advisory Group Handbook, Fact Sheet 003*. Silver Spring: American Zoo and Aquarium Association. p 1-7.
- Blaustein AR, Belden LK. 2003. Amphibian defenses against ultraviolet-B radiation. *Evol Dev* 5:89-97.
- Blaustein AR, Kiesecker JM, Chivers DP, Anthony RG. 1997. Ambient UV-B radiation causes deformities in amphibian embryos. *Proc Natl Acad Sci U S A* 94:13735-13737.
- Boutilier RG, Stiffler DG, Toews DP. 1992. Exchange of respiratory gases, ions, and water in amphibious and aquatic amphibians. In: Feder ME, Burggren WK, eds. *Environmental Physiology of the Amphibians*. Chicago, University of Chicago Press. p 81-124.
- Brattstrom BH. 1962. Thermal control of aggregation behavior in tadpoles. *Herpetologica* 18:38-46.
- Brattstrom BH. 1963. A preliminary review of the thermal requirements of amphibians. *Ecology* 44:238-255.
- Brattstrom BH. 1979. Amphibian temperature regulation studies in the field and laboratory. *Am Zool* 19:345-356.
- Brodie ED Jr. 1983. Antipredator adaptations of salamanders: evolution and convergence among terrestrial species. In: Margaris NS, Arianooutour-Faraggitaki M, Reiter RJ, eds. *Plant, Animal, and Microbial Adaptations to Terrestrial Environment*. New York: Plenum Press. p 109-133.
- Broomhall SD, Osborne WS, Cunningham RB. 2000. Comparative effects of ambient ultraviolet-B radiation on two sympatric species of Australian frogs. *Conserv Biol* 14:420-427.
- Browne RK, Odum RA, Herman T, Zippel K. 2007. Facility design and associated services for the study of amphibians. *ILAR J* 48:188-202.
- Browne RK, Zippel K. 2007. Reproduction and larval rearing of amphibians. *ILAR J* 48:214-234.
- Brust DG. 1993. Maternal brood care by *Dendrobates pumilio*: A frog that feeds its young. *J Herpetol* 27:96-98.
- Brust DG, Preest MR. 1988. The effect of temperature and hydration state on aerobic metabolism of canyon treefrogs (*Hyla arenicolor*). *Am Zool* 28:107A.
- Buchanan BW, Jaeger RG. 1995. Amphibians. In: Rollin BE, Kesel ML, eds. *The Experimental Animal in Biomedical Research*. Vol. 2. Care, Husbandry and Well-Being: An Overview of Species. Boca Raton: CRC Press. p 31-48.
- Buttemer WA. 1990. Effect of temperature on evaporative water loss of the Australian tree frogs *Litoria caerulea* and *Litoria chloris*. *Physiol Zool* 63:1043-1057.
- Campbell SS, Murphy PJ, Suhner AG. 2001. Extraocular phototransduction and circadian timing systems in vertebrates. *Chronobiol Int* 18: 137-172.
- Christian K, Parry D, and Green B. 1988. Water loss and an extraepidermal lipid barrier in the Australian treefrog *Litoria caerulea*. *Am Zool* 28: 17A.
- Clark VC, Raxworthy CJ, Rakotomalala V, Sierwald P, Fisher BL. 2005. Convergent evolution of chemical defense in poison frogs and arthropod prey between Madagascar and the Neotropics. *Proc Natl Acad Sci U S A* 102:11617-11622.
- Collins JP. 1981. Distribution, habitats and life history variation in the tiger salamander, *Ambystoma tigrinum*, in east-central and southeast Arizona. *Copeia* 1981:666-675.
- Cover JF Jr., Barnett SL, Saunders RL. 1994. Captive management and breeding of dendrobatid and Neotropical hylid frogs at the National Aquarium in Baltimore. In: Murphy JB, Adler K, Collins JT, eds. *Captive Management and Conservation of Amphibians and Reptiles*. Ithaca: Society for the Study of Amphibians and Reptiles. p 267-274.

- Daly JW. 1995. The chemistry of poisons in amphibian skin. *Proc Natl Acad Sci U S A* 92:9-13.
- Daly JW, Garraffo MH, Jain P, Spande TF, Snelling RR, Jaramillo C, Rand AS. 2000. Arthropod-frog connection: Decahydroquinoline and pyrrolizidine alkaloids common to microsympatric myrmicine ants and dendrobatid frogs. *J Chem Ecol* 26:73-85.
- Daly JW, Myers CW, Whittaker N. 1987. Further classification of skin alkaloids from Neotropical poison frogs (Dendrobatidae), with a general survey of toxic/noxious substances in the Amphibia. *Toxicon* 25: 1023-1095.
- Darst CA, Menéndez-Guerrero PA, Coloma LA, Cannatella DA. 2005. Evolution of dietary specialization and chemical defense in poison frogs (Dendrobatidae): A comparative analysis. *Am Nat* 165:56-69.
- de Vosjoli P. 1999. Designing environments for captive amphibians and reptiles. *Vet Clin N Am Exot Anim Pract* 2:43-68, v-vi.
- de Vosjoli P. 2004. *Popular Amphibians*. Lakeside CA: Advanced Vivarium Systems.
- de Vosjoli P. 2006. *Horned Frogs: Plus Budget's Frogs*. Lakeside CA: Advanced Vivarium Systems.
- de Vosjoli P, Mailloux R, Ready D. 2005. *Popular Tree Frogs* (updated ed). Lakeside CA: Advanced Vivarium Systems.
- Duellman WE, Trueb L. 1985. *Biology of Amphibians*. New York: McGraw-Hill.
- Ersparmer V. 1994. Bioactive secretions of the amphibian integument. In: Heatwole H, Barthalamus GT, eds. *Amphibian Biology*. Vol 1: The Integument. Chipping Norton NSW: Surrey Beatty & Sons. p 178-350.
- Evans SE, Milner AR, Mussett F. 1988. The earliest known salamanders (Amphibia: Caudata): A record from the Middle Jurassic of England. *Geobios* 21:539-552.
- Frost DR. 2006. *Amphibian species of the world: An online reference*. Version 4 (17 August 2006). Electronic database available (<http://research.amnh.org/herpetology/amphibia/index.php>). New York: American Museum of Natural History.
- Gabor CR, Jaeger RG. 1995. Resource quality affects the agonistic behaviour of territorial salamanders. *Anim Behav* 49:71-79.
- Gao K, Cheng Z, Xu X. 1998. First report of Mesozoic urodeles from China. *Chin Geol* 248:40-41.
- Gao K-Q, Shubin NH. 2001. Late Jurassic salamanders from northern China. *Nature* 410:574-577.
- Gao, K-Q, Shubin NH. 2003. Earliest known crown-group salamanders. *Nature* 422:424-428.
- Gehrmann WB, Ferguson GW, Odom TW, Roberts DT, Barcelone WJ. 1991. Early growth and bone mineralization of the iguanid lizard *Sceloporus occidentalis* in captivity: Is vitamin D supplementation or ultraviolet B irradiation necessary? *Zoo Biol* 10:409-416.
- Gehrmann WB. 1987. Ultraviolet irradiances of various lamps used in animal husbandry. *Zoo Biol* 6:117-127.
- Gehrmann WB. 1994. Light requirements of captive amphibians and reptiles. In: Murphy JB, Adler K, Collins JT, eds. *Captive Management and Conservation of Amphibians and Reptiles*. Ithaca: Society for the Study of Amphibians and Reptiles. p 53-60.
- Good DA. 1989. Hybridization and cryptic species in *Dicamptodon* (Caudata: Dicamptodontidae). *Evolution* 43:728-744.
- Gower DJ, Loader SP, Wilkinson M, Moncrieff CB. 2004. Niche separation and comparative abundance of *Boulengerula boulengeri* and *Scolecophorus vittatus* (Amphibia: Gymnophiona) in East Usambara forest, Tanzania. *African J Herpetol* 53: 183-190.
- Gower DJ, Wilkinson M. 2005. The conservation biology of caecilians. *Conserv Biol* 19:45-55.
- Graybeal A, Cannatella DC. 1995. A new taxon of Bufonidae from Peru with descriptions of two new species and a review of the phylogenetic status of supraspecific bufonid taxa. *Herpetologica* 51:105-131.
- Green DM. 1979. Treefrog toe pads: Comparative surface morphology using scanning electron microscopy. *Can J Zool* 57:2033-2046.
- Green DM. 1981. Adhesion and the toe pads of treefrogs. *Copeia* 1981: 790-796.
- Han BA, Kats LB, Pommerening RC, Ferrer RP, Murry-Ewers M, Blaustein AR. 2007. Behavioral avoidance of ultraviolet-B radiation by two species of Neotropical poison-dart frogs. *Biotropica* (In Press).
- Hairston NG Sr. 1987. *Community Ecology and Salamander Guilds*. Cambridge: Cambridge University Press.
- Harris RN. 1987. Density-dependent pedomorphosis in the salamander *Notophthalmus viridescens dorsalis*. *Ecology* 68:705-712.
- Hutchison VH, Dupré RK. 1992. Thermoregulation. In: Feder ME, Burggren WK, eds. *Environmental Physiology of the Amphibians*. Chicago: University of Chicago Press. p 206-249.
- Jaeger RG. 1978. Plant climbing by salamanders: Periodic availability of plant-dwelling prey. *Copeia* 1978:686-691.
- Jaeger RG. 1981. Dear enemy recognition and the costs of aggression among salamanders. *Am Nat* 117:962-974.
- Jaeger RG. 1986. Pheromonal markers as territorial advertisement by terrestrial salamanders. In: Duvall D, Muller-Schwarze D, Silverstein RM, eds. *Chemical Signals in Vertebrates 4*. New York: Plenum. p 191-203.
- Jaeger RG. 1990. Territorial salamanders evaluate size and chitinous content of arthropod prey. In: Hughes RN, ed. *Behavioral Mechanisms of Food Selection*. Heidelberg: Springer-Verlag. p 111-126.
- Jaeger RG, Forester D. 1993. Social behavior of plethodontid salamanders. *Herpetologica* 49:163-175.
- Jaeger RG, Peterson MG. 2002. Familiarity affects agonistic interactions between female red-backed salamanders. *Copeia* 2002:865-869.
- Jaeger RG, Schwarz JK. 1991. Gradational threat postures by the red-backed salamander. *J Herpetol* 25:112-114.
- Jaeger RG, Wicknick JA, Griffis MR, Anthony CD. 1995. Socioecology of a terrestrial salamander: Juveniles enter adult territories during stressful foraging periods. *Ecology* 76:533-543.
- Jenkins FA Jr, Walsh DM. 1993. An early Jurassic caecilian with limbs. *Nature* 365:246-250.
- Johnson RR. 1994. Model programs for reproduction and management: Ex situ and in situ conservation of toads of the family Bufonidae. In: Murphy JB, Adler K, Collins JT, eds. *Captive Management and Conservation of Amphibians and Reptiles*. Ithaca: Society for the Study of Amphibians and Reptiles. p 243-254.
- Kupfer A, Gower DJ, Gaucher P, Wilkinson M. 2006a. Passive trapping of aquatic caecilians (Amphibia: Gymnophiona: Typhlonectidae). *Stud Neotrop Fauna Environ* 41:93-96.
- Kupfer A, Muller H, Jared C, Antoniazzi M, Nussbaum RA, Greven H, Wilkinson M. 2006b. Parental investment by skin feeding in a caecilian amphibian. *Nature* 440:926-929.
- Lettvin JY, Maturana HR, McCulloch WS, Pitts WH. 1959. What the frog's eye tells the frog's brain. *Proc Inst Radio Eng* 47:1940-1951.
- Licht LE, Grant KP. 1997. The effects of ultraviolet radiation on the biology of amphibians. *Am Zool* 37:137-145.
- Lillywhite HB. 1970. Behavioral temperature regulation in bullfrogs. *Copeia* 1970:158-168.
- Maerz JC, Brown CJ, Chapin CT, Blossey B. 2005. Can secondary compounds of an invasive plant affect larval amphibians? *Funct Ecol* 19: 970-975.
- Maruska EJ. 1994. Procedures for setting up and maintaining a salamander colony. In: Murphy JB, Adler K, Collins JT, eds. *Captive Management and Conservation of Amphibians and Reptiles*. Ithaca: Society for the Study of Amphibians and Reptiles. p 229-242.
- Mautz WJ, Case TJ. 1974. A diurnal activity cycle in the granite night lizard, *Xantusia henshawi*. *Copeia* 1974:243-251.
- Measey GJ, Gower DJ, Oommen OV, Wilkinson M. 2003a. Mark recapture study of *Gegeneophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae) at a breeding site in Southern Kerala. *J Zool* 261:129-133.
- Measey GJ, Gower DJ, Oommen OV, Wilkinson M. 2003b. Quantitative surveying of limbless endogeic soil vertebrates—A case study of *Gegeneophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae) in southern India. *Appl Soil Ecol* 23:43-53.
- Measey GJ, Gower DJ, Oommen OV, Wilkinson M. 2004. A subterranean generalist predator: Diet of the fossorial caecilian *Gegeneophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae) in southern India. *Compte Rend Biol* 327:65-76.

- Murray DL, Jenkins CL. 1999. Perceived predation risk as a function of predator dietary cues in terrestrial salamanders. *Anim Behav* 57:33-39.
- Nace GW, Culley DD, Emmons MB, Gibbs EL, Hutchison VH, McKinnell RG. 1974. *Amphibians: Guidelines for the breeding, care and management of laboratory animals*. Washington DC: National Academy Press.
- Nessov LA. 1988. Late Mesozoic amphibians and lizards of Soviet Middle Asia. *Acta Zool Cracov* 31:475-486.
- O'Rourke DP. 2002. Reptiles and amphibians as laboratory animals. *Lab Anim* 31:43-47.
- O'Rourke DP. 2007. Amphibians used in research and teaching. *ILAR J* 48:183-187.
- Paniagua R, Fraile B, Saez FJ. 1990. Effects of photoperiod and temperature on testicular function in amphibians. *Hist Histopathol* 5:365-378.
- Parsons TS, Williams EE. 1963. The relationships of the modern Amphibia: A re-examination. *Q Rev Biol* 38:26-53.
- Pearson OP, Bradford DF. 1976. Thermoregulation of lizards and toads at high altitudes in Peru. *Copeia* 1976:155-170.
- Pough FH. 1974. Natural daily temperature acclimation of eastern red efts, *Notophthalmus viridescens* (Rafinesque) (Amphibia: Caudata). *Comp Biochem Physiol* 47A:71-78.
- Pough FH. 1980. The advantages of ectothermy for tetrapods. *Am Nat* 115:92-112.
- Pough FH. 1983. Amphibians and reptiles as low energy systems. In: Aspey WP, Lustick SI, eds. *Behavioral Energetics: The Cost of Survival in Vertebrates*. Columbus: Ohio State University Press. p 141-188.
- Pough FH. 1991. Recommendations for the care of amphibians and reptiles in academic institutions. *ILAR J* 33:S1-S21.
- Pough FH, Andrews RM, Cadle JE, Crump ML, Savitzky AH, Wells KD. 2004. *Herpetology*. 3rd ed. Saddle River NJ: Prentice Hall.
- Pough FH, Janis CM, Heiser JB. 2005. *Vertebrate Life*. 7th ed. Saddle River NJ: Prentice Hall.
- Pough FH, Wilson RE. 1970. Natural daily temperature stress, dehydration, and acclimation in juvenile *Ambystoma maculatum* (Shaw) (Amphibia: Caudata). *Physiol Zool* 43:194-205.
- Presswell B, Gower DJ, Oommen OV, Measey GJ, Wilkinson M. 2002. Scolecophidian snakes in the diets of south Asian caecilian amphibians. *Herpetol J* 12:123-126.
- Rage J-C, Roček Z. 1989. Redescription of *Triadobatrachus massinoti* (Piveteau, 1936), an anuran amphibian from the early Triassic. *Paleontographica Abt A* 206:1-16.
- Saporito RA, Donnelly MA, Hoffman RL, Garraffo HM, Daly JW. 2003. A siphonotid millipede (*Rhinotus*) as the source of spiropyrolizidine oximes of dendrobatid frogs. *J Chem Ecol* 29:2781-2786.
- Saporito RA, Garraffo HM, Donnelly MA, Edwards AL, Longino JT, Daly JW. 2004. Formic acid: An arthropod source for the pumiliotoxin alkaloids of dendrobatid poison frogs. 101:8045-8050.
- Semlitsch RD. 1985. Reproductive strategy of the facultatively paedomorphic salamander *Ambystoma talpoideum*. *Oecologia* 65:305-313.
- Seymour RS. 1972. Behavioral thermoregulation by juvenile green toads (*Bufo debilis*). *Copeia* 1972:572-575.
- Shoemaker VH, Baker MA, Loveridge JP. 1989. Effect of water balance on thermoregulation in waterproof frogs (*Chiromantis* and *Phyllomedusa*). *Physiol Zool* 62:133-146.
- Shoemaker VH, Balding D, Ruibal R, McClanahan LL. 1972. Uricotelism and low evaporative water loss in a South American frog. *Science* 175:1018-1020.
- Shoemaker VH, Hillman SS, Hillyard SD, Jackson DC, McClanahan LL, Withers PC, Wygoda ML. 1992. Exchange of water, ions, and respiratory gases in terrestrial amphibians. In: Feder ME, Burggren WK, eds. *Environmental Physiology of the Amphibians*. Chicago: University of Chicago Press. p 125-150.
- Simons RR, Jaeger RG, Felgenhaur BE. 1997. Competitor assessment and area defense by territorial salamanders. *Copeia* 1997:70-76.
- Smith EM, Pough FH. 1994. Intergeneric aggression among salamanders. *J Herpetol* 28:41-45.
- Taylor EH. 1968. *The Caecilians of the World*. Lawrence: University of Kansas Press.
- Townsend CR. 1979. Establishment and maintenance of colonies of parthenogenetic whiptail lizards. *Int Zoo Yrbk* 19:80-86.
- Townsend CR, Cole CJ. 1985. Additional notes on requirements of captive whiptail lizards (*Cnemidophorus*), with emphasis on ultraviolet radiation. *Zoo Biol* 4:49-55.
- Tracy CR. 1975. Water and energy relations of terrestrial amphibians: Insights from mechanistic modeling. In: Gates DM, Schmerl RB, eds. *Perspectives of Biophysical Ecology*. New York: Springer-Verlag. p 325-346.
- Tracy CR. 1976. A model of the dynamic exchange of water and energy between a terrestrial amphibian and its environment. *Ecol Monogr* 46:293-326.
- Tree of Life Web Project. 1995. Living amphibians. Version 01 January 1995 (under construction). Available online (http://tolweb.org/Living_Amphibians/14997/1995.01.01).
- Wake MH. 1977. The reproductive biology of caecilians: An evolutionary perspective. In: Taylor DH, Gutman SI, eds. *The Reproductive Biology of Amphibians*. New York: Plenum. p 73-101.
- Wake MH. 1978. The reproductive biology of *Eleutherodactylus jasperi* (Amphibia, Anura, Leptodactylidae), with comments on the evolution of live-bearing systems. *J Herpetol* 12:121-133.
- Wake MH. 1993. Evolution of oviductal gestation in amphibians. *J Exp Zool* 266:394-413.
- Wake MH. 1994. Caecilians (Amphibia: Gymnophiona) in captivity. In: Murphy JB, Adler K, Collins JT, eds. *Captive Management and Conservation of Amphibians and Reptiles*. Ithaca: Society for the Study of Amphibians and Reptiles. p 223-228.
- Wake MH, Dickie R. 1998. Oviduct structure and function and reproductive modes in amphibians. *J Exp Zool* 282:477-506.
- Weldon PJ, Kramer M, Gordon S, Spande TF II, Daly JW. 2006. A common pumiliotoxin from poison frogs exhibits enantioselective toxicity against mosquitoes. *Proc Natl Acad Sci U S A*. Accessed online November 9, 2006 (10.1073/pnas.0608646103).
- Whiteman HH. 1994. Evolution of facultative paedomorphosis in salamanders. *Q Rev Biol* 69:205-221.
- Wilkinson M, Nussbaum RA. 2007. Caecilian phylogeny and classification. In: Exbrayat J-M, ed. *Reproductive Biology and Phylogeny of Amphibia*. Vol 3. Gymnophiona. Science Publishers Inc. (In Press).
- Wright ML. 2002. Melatonin, diel rhythms, and metamorphosis in anuran amphibians. *Gen Comp Endocrinol* 126:251-254.
- Wygoda M. 1984. Low cutaneous evaporative water loss in arboreal frogs. *Physiol Zool* 57:329-337.
- Wygoda M. 1988. Adaptive control of water loss resistance in an arboreal frog. *Herpetologica* 44:251-257.
- Zimmermann E. 1986. *Breeding Terrarium Animals*. Neptune City NJ: TFH Publications.
- Zimmermann E, Zimmermann H. 1994. Reproductive strategies, breeding, and conservation of tropical frogs: Dart-poison frogs and Malagasy poison frogs. In: Murphy JB, Adler K, Collins JT, eds. *Captive Management and Conservation of Amphibians and Reptiles*. Ithaca: Society for the Study of Amphibians and Reptiles. p 255-266.
- Zug GR, Vitt LJ, Caldwell JP. 2001. *Herpetology*. 2nd ed. San Diego: Academic Press.