VERTEBRATES: FISH, AMPHIBIANS, REPTILES, BIRDS, MAMMALS

Contents

Amphibians

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Introduction

The basic physiology of all amphibians makes these organisms dependent on sources of freshwater during part or all of their life cycles. Specifically, these species have permeable skin that must be kept moist to enable gas exchange, and that can lead to the rapid loss of body water and resulting physiological stress in dry environments. Also, most amphibians require standing or flowing water for the development of eggs and aquatic larvae. The sources of freshwater used by these species are diverse, ranging from the moist soil beneath a decomposing log on the forest floor, to small streams and ponds that may hold water during short periods of the year, to large rivers and lakes occupied by diverse assemblages of potential competitors and predators. Likewise, the relative time that amphibian species occupy these freshwater systems can range from a brief period of explosive breeding to the entire life cycle. Consequently, the associations of amphibians with freshwater systems are best characterized as both extremely diverse and dynamic. For most species, these associations are inseparable from equally critical upland habitats, and population dynamics are influenced by processes acting in both aquatic and upland habitats.

Current knowledge of the ecology of amphibians underscores the diversity and dynamic nature of their associations with freshwater systems. In the last two decades, our understanding of the ecological differences among freshwater systems that determine which amphibian species use those systems has grown significantly. Additionally, descriptive and experimental studies have begun to examine explicitly the population and community-level consequences of the reliance on both aquatic and terrestrial systems. These studies have elucidated how characteristics of the freshwater and terrestrial habitats used by amphibians influence one another, and, consequently, why these characteristics cannot be considered separately in the context of amphibian ecology and conservation. The most striking illustrations of the importance of expanding our view of amphibian habitat requirements beyond freshwater systems have come from studies of amphibian declines that have been observed throughout the world. There remains considerable uncertainty regarding the relative importance of diverse factors implicated in these declines, including habitat degradation, pollution, disease, ultraviolet radiation, and climate change. However, many of these causal mechanisms involve a chain of impacts originating with human alterations of terrestrial systems and ending with alterations of freshwater habitats on which amphibians rely.

The objective of this article is to summarize current knowledge of how the ecology of freshwater systems affects amphibians, and why an appreciation of ecological linkages between freshwater and terrestrial systems is critical to understanding the basic ecology and conservation requirements of these species. The article is divided into two sections corresponding to the two broad categories of freshwater systems used by amphibians: lentic systems, such as ponds and lakes, and lotic systems, such as streams and rivers. Each section includes descriptions of the taxonomic groups within the amphibians generally associated with that system type, and of the natural

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history of those groups, a review of key aspects of amphibian ecology during the portion of the life cycle spent in that freshwater system, and case studies from the current literature illustrating the importance of terrestrial–aquatic linkages to the ecology and protection of amphibians that use lotic and lentic systems.

The living amphibians (class Amphibia) are divided into three orders: Gymnophiona (caecilians), Salientia (frogs and toads), and Caudata (salamanders). Frogs and toads are the most broadly distributed, occurring throughout the globe, except in Antarctica, Greenland, Arctic regions of North America and Eurasia, and some oceanic islands. The greatest diversity of frogs and toads is in the neotropical region (Central America, South America, and the West Indies), where more than 2000 species occur. Salamanders inhabit nearly all northern Temperate Zones of the world. The greatest diversity of salamanders is in North America, where representatives of 9 of the 10 extant families occur. Caecilians are found in most of the tropical regions of Southeast Asia, Africa, and Central and South America, except the dry areas and high mountains. Because caecilians are primarily terrestrial, relying on moist soils for their water requirements, this article focuses on frogs, toads, and salamanders. Although exhaustive reviews of the freshwater habitats of these groups are beyond the scope of this article, general patterns of amphibian distribution among freshwater systems are identified.

Amphibia of Lentic Systems

Amphibian Diversity and Natural History in Lentic Systems

Most frogs and toads are associated with lentic habitats, both during breeding and nonbreeding periods of the life cycle (Figures 1 and 2). Exceptions to this pattern include the tailed frog (*Ascaphus trueii*) and foothills yellow-legged frog (*Rana boylii*), stream and river-associated species found in western North America, as well as numerous stream-breeding frogs in the tropics. Among the salamanders, lentic associations predominate in the families Ambystomatidae (the mole salamanders) and Salamandridae, which is comprised of species with dry, warty skin that is commonly called newts (Figure 3). The two amphibians most commonly used as model organisms in biology labs, the African clawed frog (*Xenopus laevis*) and the Axolotl (*Ambystoma mexicanum*), a salamander native to Mexico that retains its larval form throughout its life, are primarily associated with lentic habitats.

Figure 1 An American bullfrog (*Lithobates catesbeianus*). Photograph by Dawn M Turner.

Figure 2 An American toad (*Bufo americanus*). Photograph by Kathy Bishop.

Figure 3 A great crested newt (*Triturus cristatus*). Photograph by Ian J Winfield.

In assessing differences among the lentic habitats used by these species, hydroperiod consistently emerges as an important variable. Hydroperiod is the period of time over the course of a year that a wetland, pond, or lake contains water. In lentic systems, the hydroperiod gradient ranges from ephemeral pools and ponds that may contain water for days or weeks during a rainy period of the year, to permanent lakes that support diverse communities of fish and invertebrates. Generally, the hydroperiod gradient is seen as representing a trade-off for amphibians and other organisms that occupy lentic, freshwater systems. In ephemeral ponds, competition for resources is hypothesized to be low because the short hydroperiod prevents many species from occupying these systems. However, to exploit these systems, larval amphibians must grow and develop rapidly, before the water disappears. At the other end of the hydroperiod gradient, selection for rapid development and metamorphosis is reduced, but species are more likely to experience intense competition for resources with fish and aquatic invertebrates inhabiting permanent ponds and lakes.

The proportion of the life cycle during which amphibians can be found in these lentic habitats tends to be positively related to the hydroperiod of the habitats themselves. Frogs, toads, and ambystomatid salamanders associated with ephemeral ponds tend to exhibit explosive breeding events during which migration from uplands, mating, and egg laying may occur in a few days. These migrations often occur on rainy nights, when conditions are optimal for terrestrial movement by amphibians, and range in distance from several meters to several kilometers. In areas with high densities of human development, migrating amphibians are often killed while crossing roads. To prevent these mortalities, special tunnels have been constructed beneath roads for use by migrating amphibians. Aquatic larvae (i.e., tadpoles and salamander larvae) grow and develop rapidly within ponds, and metamorphose into terrestrial juveniles within weeks or months of hatching. In contrast, adults of those species of frog, toad, and salamander associated with permanent lentic habitats are often found in these habitats both during and after the breeding season. Likewise, larvae of these species may spend several years in permanent lakes and ponds before metamorphosis occurs.

Amphibian Ecology in Lentic Systems

A great deal of what we know about the complexity of species interactions in animal communities comes from experimental studies involving amphibians that breed in temporary ponds. These studies tend to be conducted using 'artificial ponds' (e.g., cattle tanks) or enclosures within natural ponds, both of which allow for repeatable initial conditions and replication of independent experimental units. Because amphibian larvae that hatch into these ponds are under intense pressure to acquire sufficient resources for metamorphosis before drying occurs, those competitive and predator–prey interactions that do occur within and between species tend to be intense as well. Although the presence of highly efficient predators (e.g., the larvae of many ambystomatid salamanders) can eliminate other amphibian species, it has also been shown that predation risk can vary significantly among amphibian species because of minor differences in body size relative to that of the predator.

Recently, there have been major advances in our understanding of the role of phenotypic and behavioral plasticity in mediating predator–prey interactions in pond-breeding amphibian communities. It has been shown that the larvae of many potential prey species have inducible defenses – changes in behavior or morphology (e.g., tail width, coloration) that reduce predation risk, and that are only expressed in the presence of the predator. In general, these defenses come at the cost of foraging efficiency and developmental rate, and, therefore, represent a trade-off between predation risk and competitive ability. As a consequence of this trade-off, individuals that do exhibit predator-resistant phenotypes may be at higher risk of mortality because of pond drying, or may experience reduced performance following metamorphosis because of low energy reserves.

Terrestrial–Aquatic Linkages and Lentic Amphibians

The dual reliance of lentic amphibians on aquatic and terrestrial habitats is fundamental to the natural history of these organisms, but our appreciation of the consequences of this interdependence has grown significantly in the last decade. For example, in addition to providing habitat for the adults of amphibian species that breed in temporary ponds, it has recently been shown that the terrestrial habitat surrounding breeding ponds can strongly affect the growth and survival of aquatic larvae. Studies of pond-breeding frogs in eastern North America have shown that species differ in growth rate depending on canopy cover over the pond. Spring peepers (*Pseudacris crucifer*) raised on substrates and water from closed canopy ponds grew substantially slower than conspecifics in the presence of water and substrate from open canopy ponds. By contrast, wood frogs (*Rana sylvatica*) grew faster in the closed canopy treatment. This difference is thought to result from effects of canopy cover on the availability of light to algae within ponds, and the resulting variation in algal species composition or palatability that favors one species of frog over the other.

A second important set of examples of the dual dependence of lentic amphibians on aquatic and terrestrial habitats comes from studies of the role of dispersal in the population biology of these species. Because of variation over time in the habitat quality of individual ponds resulting from climate-mediated fluctuations in hydroperiod, the presence of competitors and predators, or other factors, many populations of pond-breeding amphibians rely on dispersal among ponds for long-term persistence. In these cases, dispersal acts to decouple the fate of the population from habitat conditions in any one pond, and thereby buffers the population against extinction if conditions are extremely poor in that pond in one year, or over a series of years. Because dispersal among ponds occurs through terrestrial habitat, the persistence of those species that rely on interpond dispersal is highly dependent on the hospitability of the terrestrial habitat. Consequently, natural or anthropogenic factors that reduce the likelihood of successful interpond dispersal can greatly increase the risk of population extinction in these species. Examples of such factors include forest succession, wildfire, agricultural or residential development, and timber harvest.

Amphibia of Lotic Systems

Amphibian Diversity and Natural History in Lotic Systems

In addition to the stream-breeding frogs and toads mentioned in the previous section, many salamander species are primarily associated with lotic habitats. The most species-rich family of salamanders, the Plethodontidae or lungless salamanders, includes many species that occur and breed in and along streams and rivers. Many plethodontids breed in such environments in the fall and spring, laying their eggs under rocks and logs within the stream channel. In these sites, eggs are likely to be exposed to oxygen-rich, flowing water, but unlikely to be disturbed by high-flow events. The larvae that emerge from these eggs are strictly aquatic, respiring through external gills and foraging for invertebrates and other salamander larvae within the stream channel.

Despite their common reliance on moisture for cutaneous respiration, adult plethodontid salamanders exhibit a range of associations with streams and rivers. Some species, like the northern spring salamander (*Gyrinophilus porphyriticus*; Figure 4), are highly aquatic and found under cover in the stream channel and along the wetted edge during the day, although they may move into the riparian zone on nighttime foraging bouts. In contrast, adults of the northern two-lined salamander (*Eurycea bislineata*; Figure 5), another stream-breeding plethodontid, spends summer months in the riparian zone and adjacent uplands. During this period, the northern two-lined salamander can be found under rocks

Figure 4 A northern spring salamander (*G. porphyriticus*). Photograph by Matt Ayres.

Figure 5 A northern two-lined salamander (*E. bislineata*). Photograph by Jim Andrews.

and logs during the day, and foraging on the forest floor and in understory vegetation at night. Other salamander families that include species associated with lotic habitats include the Cryptobranchidae (hellbenders and giant salamanders), Dicamptodontidae (Pacific giant salamanders), Proteidae (waterdogs and mudpuppies), and Rhyacotritonidae (torrent salamanders).

Like many groups of lotic organisms, the distributions of amphibian species associated with these habitats can be characterized by position along the stream continuum, from headwater streams to large rivers. Many species, particularly those in the family Plethodontidae, are restricted to low-order, headwater streams. Plethodontid diversity is especially high in headwater streams of the southern Appalachian Mountains of eastern North America. The cause of these headwater associations is complex, involving both evolutionary and ecological processes. However, one contributing factor is likely to be the distribution of stream fishes, which prey on salamander larvae and tend to become more abundant in larger streams and rivers. In general, amphibians that occupy larger streams and rivers attain sizes that preclude fish predation, such as the hellbender (*Cryptobranchus alleganiensis*) and mudpuppy (*Necturus maculosus*). Larvae of these species often exploit habitats within the river channel that are relatively inaccessible to fish, such as interstitial spaces among the substrate of the streambed, or lateral seepages.

Amphibian Ecology in Lotic Systems

The high species diversity of stream salamander communities in southeast North America has inspired many studies examining the ecological conditions that allow for this diversity. Although these studies have led to diverse conclusions, individual size and associated habitat requirements have been identified as important factors in promoting species coexistence. Numerous studies have shown that size is a strong predictor of the outcome of interspecific interactions, with larger species tending to outcompete or prey on smaller species. These size-mediated interactions are consistent with patterns of riparian habitat use by these species, where species exhibit largely nonoverlapping distributions relative to the stream. Specifically, larger, competitively dominant species tend to be found closer to the steam, and smaller, competitively inferior species tend to be found farther away. The mechanisms of coexistence in stream salamander larvae are not as clear as in adults. However, these mechanisms probably include differences in the timing of reproduction that reduce the likelihood that larvae of multiple species will occur together in the stream, and size-dependent differences in microhabitat use resulting in differential accessibility of refuges among streambed rocks.

Interactions with other nonamphibian species also play an important role in the ecology of amphibians in lotic systems. Interactions with predatory fish such as brook trout (*Salvelinus fontinalis*) and sunfish (*Lepomis* spp.) have received considerable attention. Numerous studies have documented strong negative effects of fish on the survival and growth of stream amphibian larvae. In addition to the direct effects of predation, it is clear that fish have strong indirect effects on amphibian larvae by forcing them into refugia among the rocks in the streambed, and thereby reducing foraging activity. On the basis of these results, the ability of many amphibians to coexist with predatory fish in streams and rivers is surprising.

Data from empirical studies point to several mechanisms that may be important in promoting coexistence of amphibians and predatory fish in lotic systems. It has been shown that larvae of the streamside salamander (*Ambystoma barbouri*) exhibit coloration similar to the substrate of the streambed, and thus reduce predation pressure through crypsis. This same species has been shown to rely heavily on refugia in the streambed to avoid predation. Larvae of several species of stream salamander have also been shown to reduce their activity and, consequently, their risk of predation in response to chemicals released into the water by fish.

For stream amphibian adults, it is clear that size and ability to use terrestrial habitat are important in promoting coexistence with predatory fish. Both of these factors allow adults to escape fish predation, either by attaining a size that exceeds the gape limit of fish, or by simply leaving the stream. In a recent study of populations of the northern spring salamander in streams of northeastern North America, there was no significant correlation between abundances of larvae and adults. This finding suggests that populations of this species can persist even when fish predation significantly reduces the abundance of larvae. Additionally, several recent observations of fish in the gut contents of adult stream salamanders suggest that the interaction between stream amphibians and fish may not be as asymmetrical as it currently appears.

Terrestrial–Aquatic Linkages and Lotic Amphibians

Like lentic species, many of the amphibians associated with lotic systems use both aquatic and terrestrial habitat over the course of their lives. For example, terrestrial invertebrates are often found to be abundant in the diets of stream amphibians, including those with highly aquatic adults. This may result in part from terrestrial invertebrates falling into the stream and subsequently being predated. However, several studies have shown that adult amphibians that are restricted to streams during the day move out into the riparian zone at night to forage. In streams where production of aquatic prey (e.g., invertebrates and smaller amphibians) is low, this behavior may be critical to the persistence of amphibian populations. Consequently, protecting these populations may require land use regulations ensuring not only that riparian habitat is protected, but also that microhabitat conditions within riparian corridors (e.g., soil moisture, air temperature, refuge availability) support this behavior.

Stream amphibians can serve as accurate indicators of the health of both aquatic and terrestrial components of the larger system. The utility of stream amphibians as indicator species results from two factors: (1) the general sensitivity of amphibians to many forms of environmental stress because they are ectotherms and have permeable skin, and (2) the tendency of lotic systems to integrate and respond to environmental conditions in the larger landscape. Evidence for this utility comes from recent studies showing strong negative relationships between stream amphibian abundances and the extent and intensity of human activities in watersheds. These studies have also shown that stream amphibians respond negatively to disturbances that occur far from the stream, as well as those that occur immediately adjacent to it. Although it is clear that stream amphibians benefit from increases in the proportion of undisturbed, forested area within watersheds, there is little information on the width of riparian buffers needed to protect these species. Additionally, the headwater streams where these species are most likely to occur often receive little or no formal protection under land and water regulations.

Several studies have shown that stream amphibians are particularly sensitive to sedimentation, a major threat to streams and rivers worldwide, and one that is closely associated with human activities such as road building, timber extraction, and residential development. Many stream amphibians use the spaces among the rocks of the streambed to forage for stream insects and to escape from fish predators. When human activities increase sediment inputs to streams, these spaces are filled with silt and sand, reducing the availability of this critical habitat. In general, little is known about how stream amphibians respond to other changes to stream habitat and water chemistry that result from human activities, such as alteration of temperature regimes, pollutant concentrations, and primary production. However, a recent study documented high concentrations of mercury in tissue from northern two-lined salamanders collected in eastern North America, and another showed that small increases in streamwater acidity can significantly reduce the activity and survival of three species of stream salamander and affect the outcome of interactions among these species.

Conclusions

Amphibians are fundamentally dependent on the supply of freshwater in the environment, but reliance on freshwater systems varies significantly among amphibian species and over the life cycle of individual species. From a scientific standpoint, this dynamic relationship with freshwater systems presents a significant challenge because it requires that processes and interactions occurring in both aquatic and terrestrial habitats be integrated into studies of these species. Restricting our attention to amphibian population dynamics and community ecology in freshwater systems, as has been the tradition, is guaranteed to lead to incomplete understanding of the basic ecology and management requirements of these species. However, along with this empirical challenge comes the potential for broad insight on the status of natural systems, both terrestrial and aquatic. As we modify the scope of our studies to address explicitly the dual reliance of amphibians on terrestrial and freshwater systems, not only will our ability to protect them improve, so will our ability to translate data on the abundance and distribution of these species into accurate information on the health and integrity of natural systems. Specific priorities for future research are suggested in the next section.

Knowledge Gaps

There is a significant geographical bias in research on amphibians, most of which focuses on North American species and their aquatic habitats. There are many historic and contemporary causes of this bias, but the most important is probably the lack of support and infrastructure for research on amphibians in many areas of the world, including many tropical areas where amphibian diversity is especially high. This bias limits our understanding of the true diversity of amphibian species, and of their natural history and ecology. It is also a major impediment to any effort to protect this diversity at the global scale.

There is limited understanding of the ecology of terrestrial stages of lentic amphibians. Most likely, this results from the difficulty of studying the terrestrial stage relative to the aquatic stage of these species. This significant knowledge gap prevents accurate assessment of the basic demography and habitat requirements of these species. For example, although we know the ecological factors that affect larval survival in many species, we have little information on the factors affecting adult survival. Consequently, there is no way to assess the relative importance to population persistence of these two sets of factors. This limitation represents a significant obstacle in efforts to isolate the causes of amphibian decline, and to prevent these declines from occurring.

Very few studies have examined how conditions that amphibian larvae are exposed to in breeding ponds affect the performance of individuals after metamorphosis, and how these carry-over effects influence population dynamics. Experiments in aquatic mesocosms and enclosures will continue to reveal diverse and fascinating ways that amphibian larvae respond to competition and predation, including new forms of phenotypic and behavioral plasticity. However, considering the amount we already know about these responses, and the rate at which studies documenting novel responses appear in the literature, we know extremely little about their population-level consequences. Only by exploring these consequences can we understand the demographic implications and evolutionary drivers of larval responses to competition and predation.

Although dispersal is known to be an important element of the population biology of many lentic amphibians, few studies have examined dispersal in lotic species. In addition to elucidating the general, demographic importance of dispersal in these species, these studies could be designed to assess the role of dispersal in promoting the coexistence of stream amphibians and predatory fish.

Studies examining the effects of amphibians on lotic food webs are scarce. Many studies have focused on interactions between stream amphibians and predatory fish, and on interactions with other amphibian species. However, relatively little is known about how stream amphibians affect the structure and composition of invertebrate communities and, consequently, primary production, litter decomposition, and nutrient cycling in streams.

There are few long-term data sets on stream amphibian populations that could be used to assess declines among these species. The majority of evidence for global amphibian declines comes from studies of lentic amphibians, yet it is likely that stream amphibians are sensitive to many of the causes of decline identified in lentic species (e.g., climate change, disease, habitat loss). Additionally, these data would reveal whether or not widespread declines are restricted to lentic species, thus providing valuable insight on both the likely causes of decline and the ecological and life history characteristics that prevent these mechanisms from impacting some amphibian species.

Further Reading

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http://www.pwrc.usgs.gov/naamp – North American Amphibian Monitoring Program.

http://www.ssarherps.org – Society for the Study of Amphibians and Reptiles.

http://www.ucmp.berkeley.edu – University of California Museam of Paleontology.