Amphibians as Models for Studying Environmental Change

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Abstract

The use of amphibians as models in ecological research has a rich history. From an early foundation in studies of amphibian natural history sprang generations of scientists who used amphibians as models to address fundamental questions in population and community ecology. More recently, in the wake of an environment that human disturbances rapidly altered, ecologists have adopted amphibians as models for studying applied ecological issues such as habitat loss, pollution, disease, and global climate change. Some of the characteristics of amphibians that make them useful models for studying these environmental problems are highlighted, including their trophic importance, environmental sensitivity, research tractability, and impending extinction. The article provides specific examples from the recent literature to illustrate how studies on amphibians have been instrumental in guiding scientific thought on a broad scale. Included are examples of how amphibian research has transformed scientific disciplines, generated new theories about global health, called into question widely accepted scientific paradigms, and raised awareness in the general public that our daily actions may have widespread repercussions. In addition, studies on amphibian declines have provided insight into the complexity in which multiple independent factors may interact with one another to produce catastrophic and sometimes unpredictable effects. Because of the complexity of these problems, amphibian ecologists have been among the strongest advocates for interdisciplinary research. Future studies of amphibians will be important not only for their conservation but also for the conservation of other species, critical habitats, and entire ecosystems.

Key Words: amphibian; amphibian decline; climate change; disease; habitat loss; pollution

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Purpose

As ecological systems are rapidly changed by human activities, good animal models are required for studying responses to ecological change. In this article, several of the most important pressures on ecological systems are discussed and examples of how amphibians have been successfully used to study the impact of these disturbances are included. The intention is not to review any of these topics in detail because the literature on the individual topics described herein has been reviewed elsewhere (e.g., Lannoo 2005; Linder et al. 2003; Semlitsch 2003a; Sparling et al. 2000). Rather, sample cases from the recent literature are described to illustrate key points that serve as a useful introductory primer to the subject matter. Where possible, readers are directed to key publications in the primary literature and reviews that provide more extensive detail on highlighted topics.

Historical Perspective on Amphibian Ecological Research

The use of amphibians as models in ecological research has a rich history. A strong early foundation in studies of amphibian natural history clearly identified attributes of amphibians that make them well suited for experimental manipulations (e.g., reviews in Duellman and Trueb 1986; Feder and Burggren 1992; McDiarmid and Altig 1999). Early research efforts provided crucial insights into amphibian diversity and population ecology, and informed our view of the novel combinations of physiological and behavioral adaptations of amphibians in different environments. During the 1970s, experimental ecologists began to take advantage of these characteristics in a quest to understand fundamental processes that influence community structure and vertebrate population dynamics. These studies revealed that amphibians were useful models for understanding how processes such as predation and competition could influence community structure (e.g., Hairston 1980, 1987; Morin 1981; Morin et al. 1983; Wilbur 1972, 1976; Wilbur and Collins 1973; Wilbur et al. 1983). Taken together, this early work inspired new generations of scientists who continue today to probe more deeply into amphibian population and community ecology, making contributions that sometimes transcend the disciplinary boundaries of amphibian biology. For example, the work of Pechmann et al. (1991) reinvigorated discussion about the importance of long-term population studies in ecology.

Importantly, the insights generated in the earliest physiological, behavioral, and ecological studies also laid the conceptual foundation for scientists to explore the utility of amphibians as models for studying applied issues that face human society. For example, work with amphibians in the 1980s and early 1990s highlighted the multifarious effects of acidification on aquatic community structure (discussed in Rowe and Freda 2000). Similar approaches, examining anthropogenic stressors on intra- and interspecific interactions, continue to be adopted today and have been instrumental in revealing the sometimes subtle and often unpredictable ways in which human disturbance can have an impact on amphibians (e.g., Boone and Bridges 2003; Boone et al. 2007; Kiesecker et al. 2001; Relyea 2005; Relyea and Mills 2001; Roe et al. 2006; Rothermel and Semlitsch 2002; Rowe et al. 1996). In this article, several of the more recent contributions of amphibian biologists to applied ecology are highlighted, including discussion of how these findings relate to broad global issues in general.

Why Use Amphibians as Models?

The continued and growing interest in amphibians as model organisms raises the following question: What is it about amphibians that makes them useful for understanding ecological processes as well as anthropogenic changes to the natural world? To help answer this question, the following important characteristics of these animals are briefly discussed below: trophic importance, environmental sensitivity, research tractability, and impending extinction.

Trophic Importance

Amphibians are critical components of both aquatic and terrestrial communities, therefore anthropogenic factors that negatively affect amphibians may influence entire ecosystems. Amphibians occupy diverse trophic niches, from planktivores to carnivores, and often serve as abundant and important prey for wildlife. Moreover, the ectothermic physiology of amphibians allows them to exploit energy-poor resources and thus serve as critical links between the lowest and highest trophic levels within a community. Certain species of amphibians represent the most abundant vertebrates in many aquatic and terrestrial communities, reaching terrestrial and aquatic densities of 2,500 and 40,000 individuals/hectare, respectively (Burton and Likens 1975; Petranka and Murray 2001). Such high biomass, coupled with the typical voracious appetites of amphibian larvae (Taylor et al. 1988) and their high conversion efficiency (Burton and Likens 1975; Grayson et al. 2005), enables amphibians to play important roles in the transfer of energy and nutrients through food webs (Beard et al. 2002; Ranvestel et al. 2004; Seale 1980; Wyman 1998). Additionally, many amphibians have complex life cycles similar to that exhibited by many invertebrates, which occupy aquatic habitats during early life stages but ultimately metamorphose into terrestrial forms. A forthcoming study indicates that a single 10-hectare isolated wetland produced >360,000 metamorphic amphibians (>1400 kg of biomass) in 1 year (Gibbons et al. 2007). This and other recent work suggest that metamorphosing amphibians provide significant energy and nutrient subsidies to surrounding terrestrial habitats (Regester et al. 2006).

Environmental Sensitivity

Amphibians possess several characteristics that may make them more sensitive to environmental disturbances than other wildlife (Rowe et al. 2003). Their permeable integument, which is critical for both gas exchange and osmoregulation, makes them particularly sensitive to changes in hydric conditions as well as contaminants and certain skin diseases. Moreover, the reliance of many amphibians on both aquatic and terrestrial habitats places them in "double jeopardy" because a disturbance to the quality or availability of either habitat can disrupt their life cycle and affect populations (Dunson et al. 1992). With regard to environmental pollution, the high conversion efficiency of amphibians should also be associated with high rates of contaminant bioaccumulation compared with other animals of similar trophic position. This theoretical framework was recently supported in a food web study using stable isotopes (Unrine et al. 2007).

Research Tractability

Unlike many other vertebrates, amphibians have numerous biological traits that make them tractable in experimental manipulations. Perhaps most importantly in a broad sense, many species of amphibians can be collected as larvae and adults in large numbers and can be housed easily in both the laboratory and outdoor enclosures or mesocosms. From an ecological perspective, the mesocosm approach to amphibian research has proved to be of paramount importance. Mesocosms, or replicated outdoor artificial systems that contain simplified self-sustaining communities (e.g., cattle tanks as temporary ponds), are advantageous because they provide a compromise between reductionistic laboratory experiments and uncontrolled, difficult-to-interpret field observations. Because they can be replicated, mesocosms permit rigorous experimental design and statistical analyses. With the exception of a few other small vertebrates (e.g., some fish species such as *Gambusia* sp.), few other vertebrates lend themselves as well to the mesocosm approach as amphibians.

Impending Extinction

Over the last 30 years, it has become clear that amphibian populations around the globe are declining at unprecedented rates (Stuart et al. 2004), representing the greatest mass extinction of land vertebrates since the dinosaurs. In the 1970s and '80s, anecdotal accounts of declines arose independently in Central America, Australia, and the western United States. By the mid- to late 1980s, the first reports were published on the subject, and this information, coupled with insights from the first World Congress of Herpetology in 1989, prompted a meeting in 1990, which the National Research Council sponsored. The years that followed were characterized by heated debate about the reality and extent of declines, promulgation of various competing theories about causes of declines, and most recently consensus that amphibian populations are in fact in great trouble for a variety of reasons. Despite continued deliberation over which environmental factors are most important in specific declines, most scientists now agree that underlying causes for declines are extremely complex and are due largely to anthropogenic disturbances (e.g., Collins and Storfer 2003; Kiesecker et al. 2001; Pounds et al. 2006). Many also agree that the health of other animals, including humans, is affected by many of the same factors that are injurious to amphibians. Therefore, it is plausible that amphibian models can serve as useful sentinels of environmental problems that other interdependent living systems face.

Why Are Amphibians Declining?

Although the precise reasons for most amphibian declines have not been completely resolved and in some cases remain enigmatic, amphibians appear to succumb to many of the same problems that affect other wildlife as well as humans. Some of the most important individual factors that are believed to be involved include habitat loss, environmental contamination, disease, climate change, introduction of exotic species, and over-harvest for human use (e.g., food, pet trade, scientific collection). However, studies on amphibians have revealed that it is the interaction among some of these factors that may be the ultimate cause of declines (Blaustein and Kiesecker 2002; Collins and Storfer 2003; Stuart et al. 2004). In the text below, the importance of the first four factors is highlighted because they have received greatest attention and have broad implications for global health, in some cases even in remote or protected portions of the world (Drost and Fellers 1996; La Marca et al. 2005; Pounds et al. 1997). Readers should note that lack of discussion of introduced species and over-harvesting is for brevity and not a statement of their lack of importance. Both factors are critical problems that wildlife face in numerous regions, and both have been linked to severe population declines in amphibians (Jensen and Camp 2003; Knapp and Matthews 2000; Vredenburg 2004).

Habitat Loss

Habitat loss represents the greatest immediate threat to most organisms around the world. Conversion of lands for human habitation, timber harvesting, and agricultural needs have decimated some of the most important ecological systems on the planet. Although many organisms succumb to loss of critical habitat, studies using amphibians have yielded new insights with direct regulatory implications for prioritizing conservation of remaining lands as well as restoring degraded habitats.

The life history of amphibians with complex life cycles has proven useful for understanding the importance of isolated wetlands. Small ephemeral wetlands such as Carolina bays in the Southeast, Delmarva bays along the Atlantic seaboard, and potholes of the US prairie lands are often viewed by the public as useless "swamps" or "puddles." In reality, however, these sites are ecological hotspots that support rich biodiversity. For example, ecological surveys on the Savannah River Site in South Carolina reveal that small wetlands represent critical breeding habitat for many species of frogs and salamanders. Remarkably, each wetland that ranges from 0.08 to 1.0 hectare supports 19 to 26 different species of amphibians (reviewed in Semlitsch 2003b). Ironically, larger permanent ponds that are valued highly by the general public often support far less amphibian diversity than ephemeral wetlands. In areas near the Savannah River Site, permanent ponds and reservoirs support only 5 to 10 species of amphibians (Scott et al. 2007). The importance of ephemeral wetlands stems from multiple factors that pertain to the natural history and population structure of amphibians, but one of the key factors is that seasonal drying eliminates or reduces the influence of key predators (e.g., fish and certain invertebrates) on amphibians (Knutson et al. 2004; Snodgrass et al. 2000; Wellborn et al. 1996). Unfortunately, current regulations in the United States reflect the common sentiment of the general public and afford little protection to wetlands smaller than 4.0 hectares (Semlitsch 2003b). Until this mindset is abolished, loss of breeding habitat will continue to plague the conservation of vertebrates and invertebrates that rely on ephemeral habitats. Mounting political pressure based on sound science by amphibian biologists may eventually help resolve this problem.

Obviously, aquatic sites fulfill only a portion of the habitat requirements for amphibians with complex life-cycles. Studies using amphibians as models have provided valuable insights into the consequences of terrestrial habitat loss. Although our knowledge of the terrestrial ecology of amphibians is much less clear than for aquatic life stages, the paucity of information is changing rapidly. A recent surge in research has revealed that amphibian terrestrial habitat requirements may be more extensive and complex than once believed. The historical view that amphibians move only small distances from ponds has been replaced with documentation of significant movements across the terrestrial landscape by numerous species (Smith and Green 2005, 2006). In addition, some amphibians appear reluctant to or incapable of using edge habitats, and some restrict movement across disturbed habitats such as old fields, possibly due to risks associated with desiccation and/or predation (deMaynadier and Hunter 1998; Rothermel and Semlitsch 2002). Such findings are causing ecologists and regulators to re-evaluate the importance of terrestrial habitat to wetland function and to redefine appropriate terrestrial buffer zones around wetlands (Gibbons 2003; Semlitsch and Bodie 1998, 2003; Semlitsch and Rothermel 2003). In addition, the realization that individual amphibians may utilize multiple wetlands in the landscape has raised important conservation questions regarding the importance of connectivity between habitats and its role in amphibian population dynamics and population genetic structure (Funk et al. 2005; Marsh and Trenham 2001; Petranka and Holbrook 2006; Smith and Green 2005).

Environmental Contaminants

Freshwater is one of the world's scarcest resources, and anything that threatens it threatens all forms of life, including humans. According to the United Nations, political tensions over clean water sources are already dangerously high in the Middle East and Africa, and such tensions will increase there and elsewhere as human populations continue to grow. Pollution is believed to be one of the most important threats to water resources, and it is one of the most pervasive insults to amphibian health around the world.

Studies using amphibian models to address questions that pertain to pollution of environmental habitats have had a profound effect on the entire field of ecotoxicology in recent years. Recognition of the threats that contaminants pose to amphibians lured ecologists to address important questions related to pollution, but the toolset these ecologists carried was much different from the toxicologists' traditional toolset. The result of this transformation is a vast literature on amphibian responses to contaminants that is permeated with ecological theory and community-based assessments (e.g., Boone and James 2005; Relyea and Hoverman 2006; Rowe and Dunson 1994; Sparling et al. 2000). The approaches of amphibian ecotoxicologists have influenced researchers who work with other organisms and raised serious questions about the relevance of traditional laboratory toxicity testing (e.g., Hopkins et al. 2004).

Extensive information now exists on the effects of pesticides, herbicides, and inorganic contaminants (metals and metalloids) on amphibians (reviewed in Linder et al. 2003; Sparling et al. 2000). Community-based mesocosm experiments have highlighted the importance of indirect influences of organic contaminants such as effects on food resources, predation, and competition (Boone and James 2005). Similar approaches have confirmed the importance of abiotic factors (e.g., hydroperiod) in determining toxicity (Roe et al. 2006). Others have demonstrated that although individuals may appear outwardly healthy, subtle latent effects can emerge later in ontogeny (Rohr and Palmer 2005) or be expressed only when transgenerational effects are considered (Hopkins et al. 2006). Amphibian models have been useful for identifying non-point sources of contamination and have provided important correlative evidence that atmospheric transport of contaminants may contribute to localized declines or extinctions of species (Davidson 2004; Davidson et al. 2002; Fellers et al. 2004; Sparling et al. 2001).

Finally, some of the responses of amphibians to contaminants have been surprising (e.g., Relyea and Mills 2001), revealing how subtle changes in ecological context can greatly modify our conclusions regarding the toxicity of compounds. Extraordinary findings are often accompanied by controversy, which was certainly the case surrounding evidence of hermaphroditism in amphibians exposed to a common herbicide (Hayes et al. 2002, 2006; Hecker et al. 2004, 2005). However, this and other controversies in amphibian ecotoxicology (Monsanto 2005; Relyea 2005) have given way to new debates regarding how chemicals are approved for use and regulated, as well as questions about the universality of dose-response paradigms in toxicology. Clearly, the use of amphibian models for studying environmental pollution has yielded new approaches and perspectives, the full impact of which has yet to be realized.

Disease and Global Climate Change

Amphibians are afflicted with a wide variety of diseases. Readers are directed to the many reviews in the literature, which include those of Carey et al. (2003) and Wright and Whitaker (2001), as well as the article "Diseases of Amphibians," which appears in this issue of *ILAR Journal* (Densmore and Greene 2007). From the earliest reports of amphibian population declines, diseases were believed to be a primary culprit. For example, trematode infections were linked to high frequencies of malformations and probable mortality in amphibians in the United States in the 1990s (Johnson et al. 1999, 2002; Sessions et al. 1999), and much work on trematode infections continues today (Belden and Kiesecker 2005; Kiesecker 2002; Taylor et al. 2005). Viral infections have been identified in several amphibian populations, and some of these diseases have proven lethal (Brunner et al. 2004; Carey et al. 2003). However, of all amphibian diseases, none have received as much attention as *Batrachochytrium dendrobatidis*, a chytrid fungus that attacks the keratinized integument of juvenile and adult amphibians, possibly disrupting respiration and osmoregulation.

In the last 15 years, chytrid fungal infections (chytridiomycosis) have been documented in Europe, Australia, Africa, Central America, and the United States (e.g., Berger et al. 1998; Bosch et al. 2001; Bradley et al. 2002; Garner et al. 2005; Lips et al. 2006; Muths et al. 2003; Weldon et al. 2004). Studies on amphibian-chytrid interactions have yielded new insights into disease ecology in general, and have raised perplexing questions about fears of emerging diseases in both wildlife and humans (Daszak et al. 2001, 2003). One of the most fascinating and disturbing aspects of chytrid fungal infections in amphibians is that based on museum collections, we know that the fungus has been present in some amphibian populations for decades, and probably longer (Daszak et al. 2005). Field surveys confirm the presence of chytrid fungus in otherwise healthy individuals where populations appear to be stable (Peterson et al. 2007). Thus, in some locations, certain amphibian species may coexist with the fungus without notable adverse effect. If this is the case, then one wonders why other species of amphibians are being forced to extinction by this disease. Studies in Australia and Central and South America have now convincingly shown that numerous species with this disease show drastic population declines (La Marca et al. 2005). In the most compelling case, investigators have tracked the progression of the fungus across Central America, where amphibian populations have declined severely and entire species have become extinct over short time periods (Lips et al. 2006 and studies cited therein). Thus, scientists are now addressing the following questions:

- Was the fungus introduced in these and other areas where vulnerable amphibian species succumbed to the disease because they lacked appropriate defenses (e.g., antimicrobial peptides; Laurance et al. 1996; Woodhams et al. 2006)?
- Alternatively, have some factors caused the fungus to become more virulent?
- Or have environmental changes caused amphibians to be more susceptible to the disease?

These questions that amphibian ecologists face are the same problems that epidemiologists and disease ecologists around the world face, as fears of global pandemics in humans and wildlife grow increasingly familiar (Daszak et al. 2001).

Many factors could lead to immunosuppression in amphibians and increase their susceptibility to diseases such as chytridiomycosis. In general, stress suppresses the immune system, so many types of human disturbance have the potential to compromise amphibian health. However, one of the most noteworthy characteristics of disease outbreaks in amphibians is that the most severe outbreaks are not occurring near large centers of human activity. Instead, relatively pristine and remote high-altitude areas in the tropics appear to be hotspots for chytrid outbreaks, amphibian population declines, and species extinctions (La Marca et al. 2005; Pounds et al. 2006). Similar amphibian declines have been attributed to other diseases in high-altitude environments in the western United States (e.g., Carey 1993). It could simply be that the disease has been introduced in these remote areas and that resident species are particularly vulnerable to the pathogen. However, other investigators have published alternative hypotheses. Given the immunosuppressive effects of contaminants (Gilbertson et al. 2003; Taylor et al. 1999), it is possible that atmospheric transport of pollutants could contribute to amphibian declines in some cases. As mentioned above, atmospheric transport of pesticides and amphibian declines in the Sierra Nevada mountains are correlated, and Rachowicz et al. (2006) have recently suggested that disease contributed to these declines as well. Using amphibian models, new evidence has recently emerged suggesting that global climate change may also play a role in disease outbreaks and subsequent population declines. After years of gathering evidence, Pounds et al. (2006) recently postulated that the declines and extinctions of amphibians in the highlands of Central and South America were caused by climatic changes that favored optimal growth of chytrid fungus. The implications of this hypothesis obviously extend far beyond the ecology of amphibian diseases.

Conclusions

When amphibian declines were widely debated in the 1990s, newspaper headlines and various scientists posed the question, Are the frogs trying to tell us something? Unfortunately, questions such as this may only be answered with confidence using hindsight. In the interim, the scientific quest for understanding the future repercussions of anthropogenic disturbances for humans and wildlife is of paramount importance if we hope to halt or reverse deleterious changes. In many cases, the questions are so complex that theoretical models are needed to provide the necessary framework for predicting future change. Nevertheless, tracking changes and testing predictions of theory in real-world circumstances are necessary for refinement of future theories and the progression of scientific thought.

Although no single animal model encompasses all desirable attributes for every environmental circumstance, amphibians have clearly become crucial to understanding the threats of habitat loss, environmental pollution, disease, and climate change on the planet as a whole. The influence of amphibian research has transformed scientific disciplines, generated new theories about global health, called into question widely accepted scientific paradigms, and raised awareness in the general public that our daily actions may have widespread repercussions. Much like research on global die-offs of coral reefs in our oceans (e.g., Carey 2005), studies on amphibian declines have provided great insight into the complexity in which multiple independent factors may interact with one another to produce catastrophic and sometimes unpredictable effects. Such problems require a shift toward interdisciplinary research, and amphibian biologists have been among the strongest advocates (e.g., Collins 2002; Collins et al. 2005) for breaching disciplinary boundaries in an effort to address the complex problems facing amphibians and other organisms in a changing world.

As we try to understand the broad implications of an expanding human population, what contributions will studies of amphibians offer in the future? The odds are that the most important work is yet to come.

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