GLOBAL DECLINES OF AMPHIBIANS

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GLOSSARY

emerging disease An infectious disease that has newly appeared in a population or that has been known for some time but is rapidly increasing in incidence or geographic range.

exotic species Organisms living in habitats where they do not occur naturally.

metapopulation A collection of local populations linked through emigration and dispersal whose long-term survival depends on the shifting balance between local extinction and recolonization.

phenological shift The relationship between a periodic biological phenomenon, such as breeding and climatic conditions.

synergistic decline factor A factor (i.e., predation, pollution, and disease) whose effect is enhanced when it is in the presence of another factor.

UV-B hypothesis The proposal that human-induced climate modification, resulting in increased levels of harmful ultraviolet radiation (UV-B), is negatively affecting amphibians.

GLOBAL DECLINES OF AMPHIBIANS refers to the phenomenon where amphibian species are experiencing severe population declines around the world. A recent assessment of the world's amphibians (Stuart *et al.*, 2004) found that 32% of 5743 species were globally threatened and that at least 43% of all species were experiencing population declines in some part of their range. These declines, more dramatic than those described for birds, mammals, or reptiles, forecast the impending extinction of many species during the coming decades. Many of these declines have occurred in protected areas and involve idiosyncratic or enigmatic causal agents. However, other declines are due to obvious reasons, particularly habitat destruction; but the number of species experiencing enigmatic declines is increasing and these have caused the greatest alarm (Semlitsch, 2003; Lannoo, 2005).

I. AMPHIBIAN BIODIVERSITY

The world's living amphibians include more than 6000 species placed in three distinct clades, the frogs and toads (Salientia), salamanders (Caudata), and caecilians (Gymnophiona). Of the three groups, frogs and toads exhibit the most varied reproductive modes and habitat associations and constitute the majority (>5300 species). Salamanders and caecilians, also diverse, have fewer species and are more restricted, but still have a widespread distribution (555 and 171 species, respectively; AmphibiaWeb, 2006). Most of the world's amphibian diversity occurs in the tropics, especially in Central and South America, but other amphibian biodiversity hotspots include sub-Saharan Africa, Madagascar, Sri Lanka, Southeast Asia, and Australia (Fig. 1). Salamanders are generally thought to be restricted to North Temperate regions, where all 10 families occur, but the largest family is well represented in tropical America, where more than 40% of all salamanders occur. Salamanders are especially abundant in North America, whereas caecilians are restricted to tropical regions.

Amphibians are often characterized as tetrapods with aquatic larvae and terrestrial adults, but alternative life histories are common. Some species of the three main clades are permanently aquatic and some of these give birth to metamorphosed offspring. In contrast, some members of all three clades (including a majority of the species of salamanders and caecilians) are strictly terrestrial and lack aquatic larvae; eggs well provisioned with yolk are laid on land and develop directly into miniatures of adults. Both frogs and salamanders may deposit eggs in arboreal microhabitats. Egg-laying sites vary greatly, and eggs, and sometimes tadpoles, of some species are transported on the legs or backs of either parent. Some members of all three clades give birth to metamorphosed young that have been nourished during development in the reproductive tract of the female, but the mode of nourishment varies, from cannibalism (in *Salamandra*), to ingested trophic oviductal secretions (caecilians), or absorption of oviductal secretions (a few frogs). Free-living larvae typically metamorphose after one season, but multiyear tadpoles are known for several species of frogs. Several salamanders never metamorphose, but remain in gilled or semigilled, pedomorphic states throughout their lives. Frogs have evolved many unusual life histories, frequently involving elimination of eggs or larvae from aquatic habitats. Eggs of different species of frogs are transferred to male vocal sacs, to compartments in the skin of the back of females, to the

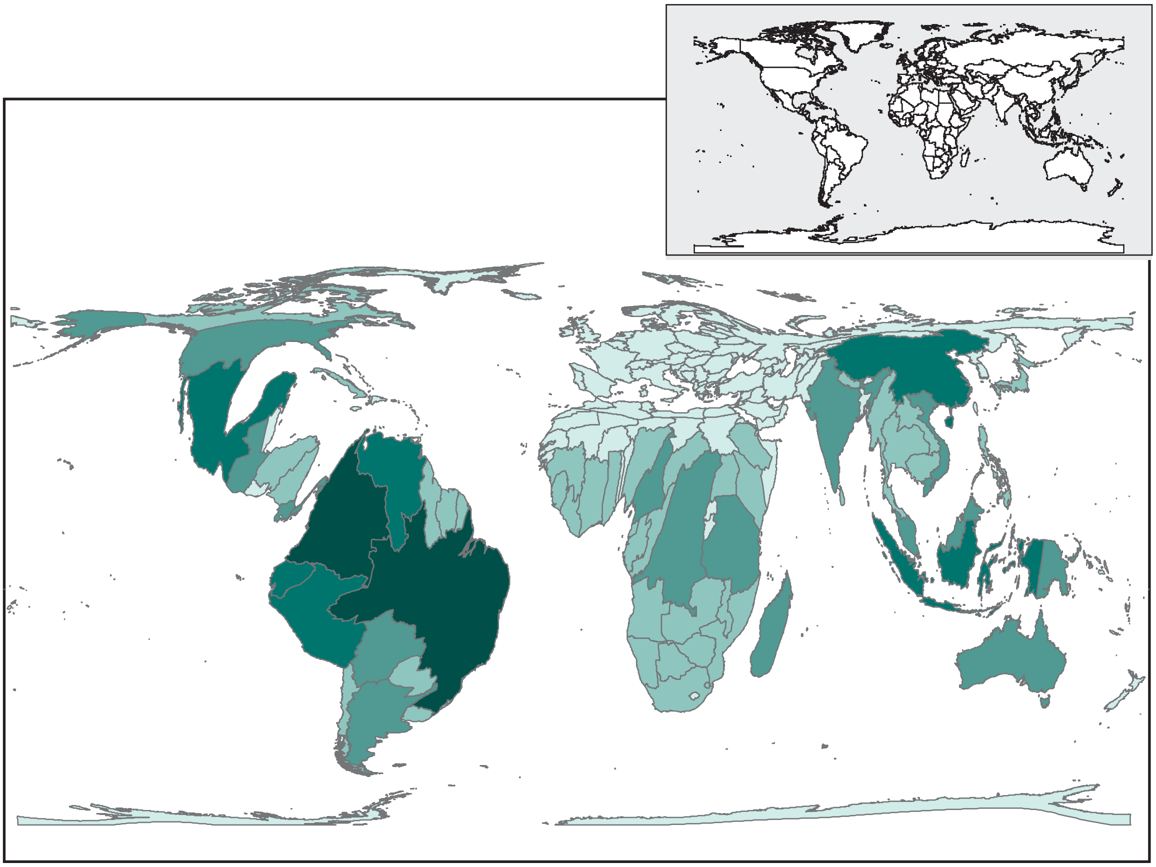

FIGURE 1 Global amphibian species diversity by country visualized using density equalizing cartograms. Country size is purposefully distorted in proportion to the number of amphibian species that occur in each country. Prepared by: M. Koo, Museum of Vertebrate Zoology; technique after Gastner and Newman (2004); data source: Stuart *et al.* (2004).

stomach, or to pouches in skin of the back of females. Larvae of salamanders, caecilians, and a few frogs are carnivorous, but most tadpoles feed on suspended or attached vegetation and detritus. Tadpoles display great diversity in behavior and microhabitat. Some are semiterrestrial burrowers and some are even semi-arboreal (McDiarmid and Altig, 1999).

Amphibians are represented in diverse aquatic and terrestrial ecosystems and are frequently important components of communities and food webs. In some parts of the world they are the dominant predator, both in terms of numbers and total mass. They are diverse in behavior. Most salamanders have the structure of a generalized tetrapod with four legs, a relatively short trunk, and a tail, but some are extremely elongated with very small limbs or only forelimbs, and some reach very large size—in excess of 1.5 m. Caecilians are limbless and their eyes are covered by skin. They have larger numbers of trunk vertebrae and are very elongated, but they either lack or have an exceedingly short tail. Frogs have a characteristic form consisting of a large head, a very short trunk, and four legs. The hind limbs contain four major segments and are elongated, suspended from elongated and specialized pelvic girdles, enabling the frogs to jump and swim. However, despite the constraints of body form, frogs are diverse in morphology, coloration, and behavior. Adult amphibians are effective predators and both salamanders and frogs have tongues specialized for rapid, long-distance prey capture. Caecilians generally feed on subterranean prey such as earthworms.

II. DIMENSIONS OF THE PROBLEM

A. Geography

The geographic extent of the declines is worldwide. The areas most affected are located in Central and South America, the Caribbean, the wet tropics of eastern Australia (Fig. 2), and western North America (Stuart *et al.*, 2004). Little is known about the status of

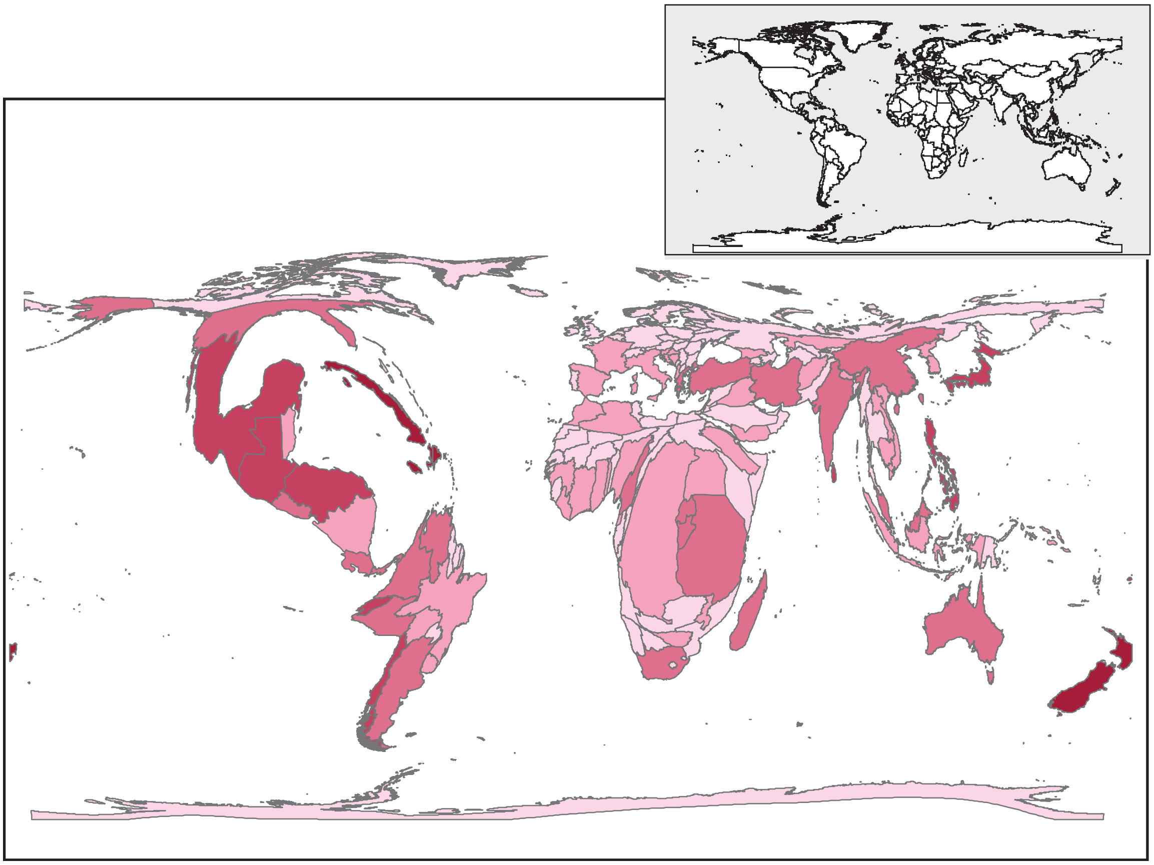

FIGURE 2 Percent of threatened amphibian species by country visualized using density equalizing cartograms. Country size is purposefully distorted in proportion to the percent of threatened amphibian species (see Fig. 1).

species in Africa and Asia due to the lack of long-term studies. The first reports of massive collapse of amphibian faunas came from montane areas in Central America and Australia. The loss of more than 50% of the species in a large tropical montane fauna (Monteverde Cloud Forest Reserve) in Costa Rica in the course of a single year (1987) was a profound shock (Semlitsch, 2003), and included the first prominent extinction (the Golden Toad, *Bufo periglenes*). Collapse of amphibian fauna in montane and lower montane Central America and South America is continuing (Lips *et al.*, 2006; Pounds *et al.*, 2006). Several species of frogs declined dramatically, some to the point of apparent extinction, in eastern Queensland, Australia, starting at about the same time (1980s). Concern has been expressed about the declines of frogs in California over many years, a phenomenon which accelerated in the 1980s and early 1990s. Now there have been reports of mainly geographically limited declines from many parts of the world.

B. Ecology

It is still too early to accurately characterize the ecology of the species that have declined, but there are some characteristics that are widely shared. Most attention has been drawn to the lower montane to montane species that are associated with streams, but there are many exceptions. Species that have aquatic breeding habits and stream-dwelling tadpoles are more likely to be in decline than species that lay eggs on land and that develop without a larval stage. In Australia, an analysis of the ecological characteristics of 40 species of frogs with an aquatic stage showed that species with stream-dwelling tadpoles are more likely to be in decline than other species (Hero *et al.*, 2005). Furthermore, independent of phylogenetic relationships, low ovarian clutch size is the ecological trait most likely to be associated with population declines. Upland species with stream-adapted tadpoles are also found to be associated with declines in lower Central and South America (Lips *et al.*, 2006; Pounds *et al.*, 2006), but in these regions entire amphibian faunas have experienced precipitous declines.

Amphibians are important members of ecosystems, and their declines are likely to have diverse, and as yet not fully understood, impacts on communities and ecosystems. Amphibians are unique among vertebrates in that many have biphasic life cycles that include fully aquatic forms (larvae) and terrestrial or semiterrestrial (adult) forms. This and the fact that they exist in so many habitats makes amphibians key components in both terrestrial and aquatic food webs. Adults are important predators, as are larval salamanders and some larval frogs; whereas more generally, tadpoles play important roles in controlling vegetation levels in both lentic and lotic ecosystems. For example, streams that have lost tadpoles may become choked with aquatic vegetation. The largely aquatic larval forms of amphibians gather productivity from aquatic habitats; and when they metamorphose into terrestrial adults, they make this productivity available to terrestrial predators. In some areas, aquatic systems are more productive than the surrounding terrestrial systems and amphibians help connect these habitats. In some cases, the loss of amphibians is cascading into declines and disappearances of their terrestrial predators (i.e., snakes). Amphibians are also important predators, for example, on aquatic insects, and their loss may greatly affect insect population dynamics.

C. Systematics

Amphibian systematics is in a state of flux and new analyses of the phylogenetic pattern of declines are in progress. Stuart *et al.* (2004) found that some taxa were more likely to be affected than others; but much more analysis is needed. What is needed in particular is to sort out the reasons for decline and then determine if there is a phylogenetic bias. For example, frogs of the genus *Atelopus* from the highlands of lower Central America and the mountains of northwestern South America have been hard-hit by declines and several species are thought to be extinct. These species also have stream-adapted larvae. Elsewhere, stream adaptation is also associated with declines, so there may be a phylogenetic bias toward ecology that is imperiling this clade. Salamanders are generally thought to be less affected than frogs, but neotropical salamanders, all members of a single clade (the supergenus *Bolitoglossa*, family Plethodontidae), are also in severe decline. Whether this is the result of their presence in a general center for declines (Central America) or of their membership in a particular clade with a life history bias (all lack aquatic larvae, a trait associated with relative immunity from declines elsewhere) is yet to be determined.

III. FACTORS RESPONSIBLE FOR THE DECLINES

Many potential causes for the widespread declines of amphibians have been proposed. In general, these can be grouped into two major categories: (i) factors general to the overall biodiversity crisis, including habitat destruction, alteration and fragmentation, introduced species and overexploitation and (ii) factors associated with amphibians that might account for declines in relatively undisturbed habitats. The first category includes relatively well-understood ecological phenomena, whereas the second includes complex and elusive mechanisms, such as climate change, increased ultraviolet radiation (UV-B), chemical contamination, spread of infectious diseases, and the causes of deformities (or malformations). The underlying mechanisms behind these factors are complex and may be working synergistically with more evident factors, such as habitat destruction and introduced species, to exacerbate declines. Many biologists believe that there are some dominant causes, such as new infectious diseases, whereas others are not convinced that there is a single overarching cause for global declines, but that many factors are threatening amphibian populations to a greater or lesser extent.

A. Habitat Degradation and Conversion

Perhaps the most obvious factor in the loss of amphibians is habitat degradation and conversion. Loss of wetlands is a major factor in temperate zones, while removal of forests is the most serious threat in the tropics. However, even in areas of high human population density, intense agricultural activity, heavy industrialization, and urbanization, such as Japan and the southern Korean peninsula, amphibians can persist and some species continue to thrive. Habitat fragmentation mostly affects widespread species and those that have natural metapopulation structures. Many amphibians, especially terrestrial species with direct development and no larval stages, are typically highly structured genetically, with much cryptic diversity, and fragmentation leading to extensive loss of biodiversity even if species fragments persist. Some habitat changes are subtle and have unexpected effects. Fire suppression in parts of western North America has led to encroachment of forests into breeding sites, resulting in shading that has negative effects on tadpole development.

A major factor in habitat degradation is pollution from agricultural pesticides and fertilizers (Hayes *et al.*, 2002). There is now extensive documentation both of direct effects and of synergistic interactions with other factors (see below). In northern zones, acid precipitation has been shown to affect species at the limits of their ranges.

B. Impact of Exotic Species

The establishment and spread of exotic species are a major threat to worldwide biodiversity, and there are many examples of amphibians being affected (Kats and Ferrer, 2003). Exotic species affect amphibians as competitors, predators, and as vectors for parasites and disease. Nonnative or exotic amphibians are responsible for many of the declines of native amphibians. The North American bullfrog (*Rana catesbeiana*) has been transported around the world by humans mostly for food. In California, bullfrogs were introduced after native red-legged frogs (*R. draytonii*) were hunted to low numbers in the nineteenth century. Wild populations of nonnative bullfrogs now eat and outcompete native red-legged frogs and foothill yellow-legged frogs (*R. boylii*), both of which are in decline. In the last several decades, nonnative bullfrogs escaped from farms in Venezuela and established wild populations in areas where native frog populations collapsed (several species of the genus *Atelopus*). Some native amphibians are infected with chytridiomycosis, a disease caused by a fungal pathogen. Bullfrogs appear to be resistant to chytridiomycosis, and may act as carriers for the disease. In Australia, sugarcane farmers introduced cane toads (*B. marinus*) in an effort to control insect pests. Unfortunately, the nocturnal cane toads do not control the largely diurnal pests. Since the first introductions in the late 1800s, cane toads have spread throughout the eastern portion of Australia where they act as both competitors and predators of native amphibians. Additionally, the toads produce toxic defensive compounds in their skin, and they are often deadly to predators that eat them, such as native amphibians, mammals, birds, and snakes. Nonnative populations of African clawed frogs (*Xenopus leavis*) have also been widely established around the world. They are prolific, highly competitive and, like the bullfrog, are implicated in the spread of chytridiomycosis to native species of amphibians.

Fish are generally dominant species in aquatic systems, but unlike most amphibians, they are bounded by natural aquatic barriers such as waterfalls, dry land, etc. Humans, however, have introduced fish varieties to new aquatic habitats and this has had devastating consequences for some amphibians, especially those that evolved without fish predators. A well-studied example is the introduction of trout into historically fishless freshwater systems. Trout (Salmonidae: *Onchorhychus* sp., *Salmo* sp.) are restricted to cold mountain streams in North America and Europe but have been widely introduced to every continent on Earth except Antarctica. Aquatic systems in entire mountain ranges have been altered. For example, in California, prior to the mid-1800s, more than 99% of the lakes and ponds in the Sierra Nevada above 2100 m were fishless. Historical accounts from the Museum of Vertebrate Zoology (Grinnell and Storer, 1924) state that the mountain yellow-legged frog (*R. muscosa*) was once the most common vertebrate in these high-elevation ponds and lakes. Since the mid-1800s, trout have been introduced throughout the Sierra Nevada for sport fishing. Now, more than 90% of these naturally fishless lakes contain nonnative trout. The mountain yellow-legged frog, which is adapted to living in environments without any fish, has declined dramatically, and while there are many potential causes for the decline of this species, field experiments have shown that removal of introduced trout from entire lakes can lead to recovery of local populations (Vredenburg, 2004).

C. Infectious Diseases

Infectious diseases have been associated with collapsing amphibian populations on several continents including Central America and Australia (Berger *et al.*, 1998). Viruses, bacteria, water molds, fungi, and trematode parasites are among the diverse agents associated with varying levels of mortality and population decline. Viruses belonging to the family Iridoviridae have been associated with mass mortality in the common frog (*R. temporaria*), the Sonora tiger salamander (*Ambystoma tigrinum*), and other species in both captive and wild populations. The bacterial pathogen characteristic of red-legged disease, *Aeromonas hydrophila*, has been reported in amphibians in wild populations for several decades, and a pathogenic water mold, *Saprolegnia ferax*, appears to be largely responsible for egg mortality in several western North American amphibians. Trematode infestation has been implicated in limb deformities in the pacific tree frog (*Pseudacris regilla*) and several other species of amphibians, but so far no population declines have been tied to trematode infestations. Extinctions of several Wyoming Toad (*B. baxteri*) populations are thought to be primarily due to the parasitic fungus *Basidiobolus ranarum*. The disease that has generated the most alarm amongst herpetologists and conservation biologists is chytridiomycosis caused by the pathogenic fungus *Batrachochytrium dendrobatidis* (Berger *et al.*, 1998). The disease played a major role in the amphibian population collapse in Central and South America (Berger *et al.*, 1998; Lips *et al.*, 2006), and is implicated in declines in Spain, Australia (Berger *et al.*, 1998) and California (Rachowicz *et al.*, 2006). It is unknown whether chytridiomycosis is an emerging disease that has recently been spread to new habitats, or if it previously coexisted with amphibians but either the pathogenicity has recently increased or the amphibian immune function has recently decreased.

D. Factors Associated with Global Climate Change

There is a growing suspicion among ecologists that amphibians may be more sensitive to climate change than other vertebrates, notably such as birds, because they are more likely to show habitat and microhabitat specialization and because they are significantly less vagile.

1. Elevated UV-B Increased Ultraviolet Radiation

Global atmospheric changes caused by anthropogenic activities are well documented and one result is a reduction of stratospheric ozone resulting in an increase in the amount of biologically damaging UV-B reaching the Earth's surface. The increase in UV-B may be causing increased mortality rates in amphibians and this could help explain enigmatic declines in protected areas. Most of the work testing this hypothesis has focused on comparing egg-hatching rates in species that lay their eggs in shallow, exposed breeding sites subject to high levels of UV-B. Field experiments have concluded that many species are sensitive (Blaustein *et al.*, 1998); however, not all species that are sensitive are in decline and recent studies suggest that interactions between UV-B and factors such as water chemistry, seasonal variations in breeding, and amount of precipitation are important.

2. Establishment of Conditions Favorable for Fungal Growth

Several studies have suggested that a change in climate may make conditions favorable for the spread of amphibian diseases and parasites. These may then overwhelm frog immune systems causing death. For example, in the America tropics 67% of the 110 species of Harlequin frogs in the genus *Atelopus* declined soon after unprecedentedly high mean air and sea surface temperatures (Pounds *et al.*, 2006). While warmer conditions directly affect frogs, one hypothesis is that a warming climate leads to more cloud formation, which could favor the growth of the fungal pathogen. The hypothesis states that by increasing the average lowest nighttime temperature and lowering the average daytime maximum temperatures, the pathogen experiences optimal growth temperatures.

3. Threats from Shifts in Weather Patterns

Many species react to changes in climate by shifting their distributions either latitudinally or altitudinally. Good evidence exists that some lowland butterflies in western North America are moving both to higher elevations and higher latitudes, presumably tracking shifting resources that change as climate changes. In contrast, in the American tropics there is evidence that climate change has initiated precipitous declines in amphibians, even within a single season (Pounds *et al.*, 1999). Amphibians, especially those in tropical regions, are narrowly distributed, for example they are restricted to specific and often narrow elevational belts on mountains that are themselves isolated. There may be no place to go when climate becomes warm or dry, except higher up the mountain. Species already at the top of such habitats are literally pushed off the mountain, into extinction. Other species may be limited in their movements to the north or south, by ranges fragmented by habitat conversion, or by barriers such as rivers that effectively stop range expansion.

Global climate change has diverse direct effects on amphibians. In Central America, the cloud line has risen several hundred meters; and the immediate effect was a drought of unusual severity in a high-elevation cloud forest in Costa Rica, which has been implicated in the disappearance of 20 out of the 50 species of amphibians known from the site, including a local endemic, the Golden Toad, *B. periglenes* (Pounds *et al.*, 1999).

In temperate zones, one documented effect of climate change has been the earlier breeding of some species in the northern parts of their ranges. The long-term implications of this phenological shift are still unclear.

E. Synergistic Effects

Many factors by themselves pose severe threats to amphibian survival, but more insidious and much harder to comprehend are synergistic interactions between factors. Many synergisms have been proposed (Pounds *et al.*, 1999; Blaustein and Kiesecker, 2002). The effects of infectious diseases may be greater in the presence of elevated UV-B or of chemical pollutants (e.g., pesticides or fertilizers), which may compromise immune systems. Unusual weather conditions might enhance the impact of different stressors. The link between climate change and pathogen growth conditions in Central America, mentioned above, may be enhanced by the presence of additional stressors like high environmental loads of pesticides in the area. In California, pesticide drift from the heavily agricultural Central Valley has been linked to the disappearance of high-elevation frog populations, possibly by enhancing the effects of chytrid infection on populations already weakened by interactions with exotic predators (introduced trout). Many other kinds of synergistic effects have been suggested. Synergisms are likely to pose a major threat to the continued existence of many amphibians.

IV. CHALLENGES AND OPPORTUNITIES FOR THE FUTURE

Perhaps the main surprise associated with amphibian declines is that so many of the most dramatic instances have taken place in protected areas, such as the great national parks of the Sierra Nevada of California, the Monteverde Cloud Forest Preserve in Costa Rica, and protected areas in Australia, to give three prominent examples. Thus, the standard conservation approach of purchasing and protecting land and habitats is unlikely to assure survival. Instead, conservation strategies must involve researchers with diverse talents in the fields of infectious disease ecology, reproductive biology, endocrinology, immunology, and pollution ecology. Natural historians are critical components of any conservation strategy, for it is their expertise that may provide insight into patterns of survival and recovery of once infected organisms, for example. *Ex situ* strategies increasingly seem to be essential, but captive breeding is difficult and expensive and careful thought must be given to the selection of the candidate species (e.g., phylogenetic, ecological, and behavioral diversity should be represented). A necessary element is information exchange and discussion among specialists and generalists to attempt to formulate new pathways for understanding, and community action to counteract the very real threats facing this ancient group of organisms.

A. Mitigation of Habitat Changes

Wetland restoration holds great promise for recovery of many amphibian species. Alteration of wetlands by humans has had one of the most substantial effects on amphibian populations. Wetlands are important components of the Earth ecosystems as they provide vital ecosystem services (i.e., water purification). Mitigation in wetlands not only benefits humans directly by helping restore clean water systems, but also provides an important habitat for many species of amphibians.

B. Removal of Exotic Species

As more amphibian populations collapse, reversing these declines is becoming increasingly urgent. The removal of exotic species is something that has been proved to work in several systems, but is not yet widely used. For example, removal of exotic fishes has had positive benefits for amphibians in Spain, Chile, and in several areas within the United States. In California, removal of nonnative trout from entire lakes in the Sierra Nevada led to the rapid recovery of threatened mountain yellow-legged frog populations (Vredenburg, 2004).

C. Attenuation of Infectious Agents

Study of disease ecology in wild amphibians has only recently gained a lot of attention. Disease ecology seeks to understand the mechanisms that lead to disease outbreaks in natural systems. In some cases, museum collections can be used to look back in history for pathogens in order to see whether they were present then or were more common compared to today. The vast increase in connectivity through global trade between continents may be linked to many of these outbreaks. Precautions like disinfection and quarantine programs and the prevention of human movement of disease vectors (i.e., live bullfrogs) must be taken to help lower the probabilities of future outbreaks.

D. Captive Breeding

While some biologists view captive breeding as a last-resort conservation action, the International Union for the Conservation of Nature and Natural Resources (IUCN) endorses captive breeding as a proactive conservation measure, one that should be initiated while a species is still available to allow for a husbandry learning curve.

V. IMPLICATIONS FOR THE BIODIVERSITY CRISIS IN GENERAL

Amphibian declines may be the window into the future of what we can expect as humans continue to alter the environment on a global scale. Only now are government officials finally willing to acknowledge that humans have caused so much damage to the environment that they are even affecting global climate change. We do not think that amphibians are special or unusual. In our case, they are simply the organisms we chose to study, and there is no *a priori* reason to think that they are exceptions. We can no longer lock up nature and expect it to care for itself. Ironically, we may not only be a primary source of the problems facing amphibians, but also, their main hope for the future. It is too early to tell if amphibians have lessons for conservation strategies in general, but it is very clear that we are now facing extinctions on a massive scale, well beyond anything we have ever experienced.

See Also the Following Articles

AMPHIBIANS, BIODIVERSITY OF • CAPTIVE BREEDING AND REPRODUCTION • CLIMATE CHANGE AND EXTINCTIONS • DISEASES, CONSERVATION AND • ENDANGERED AMPHIBIANS • ENDANGERED REPTILES AND AMPHIBIANS • INTRODUCED SPECIES, EFFECT AND DISTRIBUTION OF • ULTRAVIOLET RADIATION

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