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Global Declines of Amphibians

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Glossary

Cryptic diversity Populations that are nearly identical to others in morphology but have significant differences in their DNA sequences, indicating isolation for an extended period of time; these represent unique evolutionary lineages that should be preserved.

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.

Metapopulation Collection of local populations linked through emigration and dispersal whose long term survival depends on the shifting balance between local extinction

Exotic species Organisms living in habitats where they do

Taxonomist Scientist whose work involves the discovery, description, and classification of life forms, based on the Linnean hierarchical system.

Introduction

Global declines of amphibians refer to the phenomenon of the population declines and even extinctions of amphibian species around the world. Assessments of the world's amphibians (Stuart et al., 2004, 2008) found that nearly a third of the known species of amphibians are globally threatened with extinction and that at least 42% of known amphibian species are experiencing population losses. The rapidity and extent of these declines, far more dramatic than those described for birds, mammals, or reptiles, forecast impending extinction of numerous amphibian species during the coming decades. Many of these declines have occurred in protected areas where the causes have remained enigmatic. 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. Although climate change has been invoked as a potential contributing factor (e.g., Pounds et al., 2006), evidence is mounting that epidemics of infectious disease may be primarily responsible for many of these catastrophic declines (Collins and Crump, 2009). The greatest threat is presented by a virulent fungal pathogen that can cause the infectious disease chytridiomycosis, which has decimated entire assemblages of amphibians worldwide. This pathogen, Batrachochytrium dendrobatidis, is responsible for what may well be the greatest disease-caused loss of biodiversity in recorded history, having caused population crashes or extinctions (often within a single year) of at least 200 species of frogs, even in relatively undisturbed, remote habitats. Compounding the crisis, amphibians suffer from relatively low levels of conservation effort compared to other vertebrate taxa. Although amphibians have survived a number of mass global extinctions throughout their 200 million year history, the speed and magnitude of this loss in amphibian biodiversity supports the idea that the earth may be now in the midst of a sixth mass extinction, similar to that which wiped out the nonavian dinosaurs.

Amphibian Biodiversity

not occur naturally.

and recolonization.

The world's living amphibians include over 6800 species placed in three distinct clades, the frogs and toads (Anura), salamanders (Caudata), and caecilians (Gymnophiona). Of the three groups, frogs and toads exhibit the most varied reproductive modes and habitat associations and comprise the majority of amphibians (over 6000 species). Salamanders and caecilians, also diverse, have fewer species and are more restricted in distribution, but are still widespread (more than 600 species and nearly 200 species, respectively, based on the online resource AmphibiaWeb 2010). Most of the world's amphibian diversity occurs in the tropics, especially in Central and South America; other amphibian biodiversity hotspots include sub-Saharan Africa, Madagascar, Sri Lanka, SE Asia, New Guinea, and Australia (Figure 1). Salamanders are generally found in North Temperate regions, where all 10 families occur, but the largest family (Plethodontidae) is well represented in tropical America, where more than 40% of all salamander species occur. Salamanders are especially abundant in North America, whereas caecilians are restricted to tropical regions. In contrast, frogs range in distribution from the Arctic zone to the southern tips of South America and Africa.

Amphibians are often characterized as tetrapods with aquatic larvae and terrestrial adults, but alternative life histories are common. Some species of the three main amphibian clades are permanently aquatic. In contrast, other members of all three clades (including a majority of the species of salamanders and caecilians and more than a thousand frogs) are strictly terrestrial and lack aquatic larvae; eggs well provisioned with yolk are laid on land and develop directly into miniatures of adults. Some members of all three amphibian clades are live-bearers, giving birth to metamorphosed young that have been nourished during development in the reproductive tract of the female. Some salamander species never metamorphose, but remain aquatic in gilled or semi-gilled states throughout

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Figure 1 Global amphibian species diversity by country, visualized using density equalizing cartograms. Each country's shape is purposely distorted in proportion to the number of amphibian species per country area (square kilometer) using the cartogram technique after Gastner and Newman (2004). (Data source: AmphibiaWeb (website accessed 17 November 2010).)

life. Frogs have evolved many unusual life histories that avoid aquatic habitats for depositing eggs or larvae, such as transferring eggs to male vocal sacs, to pouches in the skin of the back of females, or even to the stomach.

Most salamanders have the structure of a generalized tetrapod with four legs, a relatively short but flexible 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 or bone. Caecilians have high numbers of trunk vertebrae and are very elongated, but they either lack entirely or have an exceedingly short tail. Frogs are also tetrapods but have a more specialized form that generally enables jumping (although some species walk, hop, or burrow), because they lack a tail, have a very short and stiffened trunk, and have relatively elongated legs and feet.

Adult amphibians are effective predators and both salamanders and frogs have tongues specialized for rapid, longdistance prey capture. Caecilians generally feed on subterranean prey such as earthworms. Amphibians are represented in diverse aquatic and terrestrial ecosystems and frequently are important components of communities and food webs. In some ecosystems, they are the dominant predators, both in terms of numbers and total biomass.

Dimensions of the Problem

Geography

The geographic extent of amphibian declines is worldwide (see Fisher et al., 2009 for a longer review). Areas most strongly affected are located in Central and South America, the Caribbean, the wet tropics of eastern Australia (Figure 2), and western North America (Stuart et al., 2008). The islands of the Caribbean and Pacific have some of the highest percentages (up to 100%) of endemic species that are threatened or endangered, but have relatively few species. Less is known about the status of species in Africa and Asia. Nonetheless, some species-rich countries have alarmingly high percentages of threatened and endangered species (e.g., 70% for Sri Lanka, based on the online resource IUCN 2010). The first reports of massive collapse of amphibian faunas came from montane areas in Central America and Australia. The loss from the protected Monteverde Cloud Forest Reserve in Costa Rica of more than 50% of the amphibian species within the course of a single year (1987) was a profound shock, 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 ongoing. In Australia, declines began in the 1970s in southern Queensland and Tasmania and accelerated in the 1980s. In Europe, die-offs were observed beginning with Spain in the mid-1990s. Concern has been expressed over declines of frogs in the western US for many years, and in the 1980s and early 1990s population collapses were observed in relatively undisturbed areas such as Yosemite National Park. Amphibian declines have since been reported from many parts of the world.

Ecology

In characterizing the ecology of species that have declined, most attention has focused on high- or mid-altitude species that are associated with streams, have small ranges (implying higher habitat specificity), and low reproductive rates, but there are many exceptions. Species that have aquatic breeding habits and stream-dwelling tadpoles have generally experienced sharper declines than species that lay eggs on land and that develop without a larval stage (direct developers). However, direct-developing species are not exempt; in Puerto Rico, for instance, many species of direct-developing frogs have declined and some may be extinct.

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 lifecycles that include both fully aquatic (larvae) and terrestrial or semi-terrestrial (adult) forms. This makes amphibians key components in both terrestrial and aquatic food webs. Aquatic systems are more productive than the surrounding terrestrial systems in some areas, and amphibians help to link these two types of habitats. Although larval salamanders are carnivorous, tadpoles (larval frogs) are generally herbivorous and play important roles in controlling vegetation levels in both lentic (still water) and lotic (flowing water) ecosystems. For example, streams that have lost tadpoles can become choked with aquatic vegetation. Tadpoles compete with aquatic insect larvae for food, and loss of tadpoles alters the macroinvertebrate community composition. Adult amphibians may prey on a variety of items depending on their size and lifestyle; burrowing caecilians generally consume earthworms, whereas terrestrial frogs and salamanders may consume anything from tiny terrestrial leaf-litter dwelling insects such as springtails, mites, and ants to other vertebrates (including other amphibians). Amphibian loss affects predator populations (e.g., snakes) and may also affect the population dynamics of prey taxa such as insects.

Systematics

Amphibian systematics is in a state of flux, adding to the challenge of assessing and tracking the scope of global decline. There are insufficient numbers of amphibian taxonomists, which hinders fundamental conservation assessments. Currently, amphibian taxonomists are concentrated in the more species-poor but wealthier countries; there is increasing recognition of the need for established resident taxonomists in species-rich regions. A new generation of taxonomists is developing in Asia and South America, but there are gaps in expertise in species-rich regions such as Africa. The marked recent increase in amphibian biologists has accelerated field studies in remote areas and discovery of many new species. Ironically, during a time of crisis for the world's amphibians, the number of described species has risen from 4000 in 1985 to over 6800 today.

Phylogenetic patterns of amphibian declines are not well understood. Some clades appear to be especially susceptible to declines. For example, frogs of the genus *Atelopus* from the highlands of lower Central America and the mountains of

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Figure 2 Percent of threatened and endangered amphibian species by country visualized using density-equalizing cartograms. Country size is purposely distorted in proportion to the percentage of threatened and endangered amphibian species, not including introduced species using the cartogram technique after Gastner and Newman (2004). (Data sources: AmphibiaWeb (website accessed 17 November 2010) and IUCN (website accessed 30 September 2010).)

northwestern South America have been hard-hit by declines; nearly 80% of described Atelopus species have been classified as critically endangered or extinct. These species have streamadapted larvae. Elsewhere stream adaptation is also associated with declines, suggesting a phylogenetic bias within the clade containing Atelopus. Although salamanders seem to show less evidence of declines than frogs, neotropical salamanders (both ambystomatids and plethodontids) are experiencing severe declines. The vast majority of tropical salamanders are plethodontids, members of a single clade known as bolitoglossines, and declines of Mexican and Guatemalan species have been well documented (Rovito et al., 2009). Although a number of studies have found a phylogenetic component to amphibian declines, data from one of the best-studied amphibian mass mortality events in Panama indicated that decline and extirpation were random with respect to phylogeny (Crawford et al., 2010). Assessing the amount of phylogenetic diversity lost in declines and extinctions is also complicated by the fact that the amphibian fauna is not fully known in many species-rich areas.

Factors Responsible for the Declines

Potential causes for the widespread declines of amphibians can be grouped into two major categories: (1) factors general to the overall biodiversity crisis, including habitat destruction, alteration and fragmentation, introduced species, and overexploitation and (2) 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 less well understood agents with complex underlying mechanisms, such as infectious diseases, climate change, increased UV–B radiation, chemical contaminants, and the causes of deformities. Habitat loss has played a major role, as has the infectious disease chytridiomycosis, but amphibian populations often face many simultaneous threats and synergistic interactions between different threats may exacerbate declines.

Habitat Degradation and Land Conversion

Perhaps the most obvious factor in the loss of amphibians is habitat degradation and land conversion. Although some amphibians are able to not only persist but thrive in urbanized or agricultural areas, many species require undisturbed (or relatively undisturbed) habitat. Loss of wetlands is a major factor in temperate zones, whereas removal of forests is the most serious threat in the tropics. Habitat fragmentation, where forest remnants persist but are separated by disturbed habitat such as pasture, is a serious issue for widespread species and in those that have natural metapopulation structures. Many amphibians, especially terrestrial species with direct development and no larval stages, are typically highly structured genetically and have cryptic diversity; in this case, habitat fragmentation leads to extensive loss of biodiversity as populations die out, even if species fragments persist. Human-induced disconnection between habitats used by different life history stages makes breeding

migrations risky and may account for some of the reason why species with aquatic stages are declining more than strictly terrestrial species. 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, with the resulting increase in shade having negative effects on tadpole development in some species.

Habitat degradation from pollution from agricultural herbicides, insecticides, and fertilizers impacts amphibians with aquatic life stages, either directly or by synergistic interactions with other factors (Hayes *et al.*, 2010). Chemical pollutants can directly kill larvae at certain concentrations, but even sublethal concentrations can affect behavior, reproduction, and life history, and can reduce the food supply (Relyea and Diecks, 2008). In some species, stress can magnify the effects of chemical doses that would normally not be lethal. We remain far from having a full understanding of the impacts of additives by humans to the environment on amphibians.

Impact of Exotic Species

The establishment and spread of exotic species are major threats to worldwide biodiversity and there are many examples of amphibians being affected. Exotic species can affect amphibians as competitors, predators, and as vectors for parasites and diseases. Nonnative amphibians may have contributed to many of the declines of native amphibian species. The bullfrog (Rana catesbeiana) is native to eastern North America but has been transported around the world by humans, mostly for human consumption. In California, wild populations of nonnative bullfrogs now eat and out-compete red-legged frogs (Rana draytonii) and foothill yellow-legged frogs (Rana boylii), both of which are in decline. In the last several decades, nonnative bullfrogs have escaped from commercial frog farms, particularly in South America, and established wild populations in areas where native frog populations collapsed. Although many native amphibians are dying from chytridiomycosis, bullfrogs appear to be resistant and are thought to act as carriers for the disease.

In Australia, sugar cane farmers introduced cane toads (*Bufo marinus*) in an effort to control insect pests, but the nocturnal cane toads do not control the largely diurnal pests. Since the first introductions in the late 1800s, cane toads have spread rapidly throughout eastern and more recently northern portions of Australia where they act as both competitors and predators of native amphibians, as well as apparently introducing pathogens and parasites. Cane toads produce toxins at all life stages, and ingesting cane toad eggs, larvae, or metamorphs is fatal to both larval and adult native Australian amphibians.

Another invasive amphibian species is *Xenopus laevis*, the African clawed frog, which is now widely established around the world. These fully aquatic frogs are prolific, highly invasive, and prone to *Bd* infection but resistant to chytridiomycosis. Like bullfrogs, African clawed frogs have been implicated in the spread of both chytridiomycosis and ranaviruses to native amphibians. They also out-compete native

amphibians, which decrease reproduction in ponds invaded by feral *Xenopus laevis*.

Fish are generally dominant species in aquatic systems and human-mediated introduction of fishes to new aquatic habitats has often had devastating consequences, especially for those amphibian species that evolved without fish predators. Fish-naive amphibian species may fail to recognize predator cues or lack behavioral responses to avoid fish predation. Introduced fish such as mosquitofish, carp, and trout have been shown to prey on amphibian eggs and larvae. Trout are native to cold mountain streams in North America and Europe but have been widely introduced to every continent except Antarctica. In the Sierra Nevada of California, more than 99% of the lakes and ponds above 2,100 m were fishless prior to the mid-1800s. Since then, trout have been introduced into more than 90% of Sierra Nevada lakes for sport fishing. Mountain vellow-legged frogs, once the most common vertebrates in these high-elevation ponds and lakes, are adapted to life in environments without any fish and have declined dramatically with the introduction of trout. Field experiments showed that removal of introduced trout from entire lakes could lead to recovery of local mountain yellow-legged frog populations. However, soon after this discovery chytridiomycosis was detected in the Sierra Nevada and has spread rapidly, further endangering the last remaining populations of these species. Paedomorphic salamanders (which retain certain larval traits and remain aquatic into adulthood) can also be particularly vulnerable to fish predation. Another introduced aquatic predator known to feed on amphibian larvae is the red swamp crayfish (Procambarus clarkii, which is native to North America but has been introduced on all continents except for Antarctica and Australia) and is associated with amphibian population collapses in Portugal.

Fish compete with amphibians (and birds) for aquatic insect prey. Presence of introduced insectivorous fish such as trout in montane lakes of northern California was correlated with decreased diversity of native aquatic insects and far less insect emergence. Removing introduced trout from northern California lakes led to the recovery of invertebrate populations.

Introduced species can exert effects on native amphibians indirectly by altering the habitat. Exotic fish such as carp or tilapia can increase water turbidity in shallow water bodies, which decreases productivity and is thought to be one factor in the decline of native axolotls in Mexico.

Infectious Diseases

Infectious diseases have been associated with collapsing amphibian populations almost everywhere that amphibians occur (Fisher *et al.*, 2009; Gray *et al.*, 2009). Most of the reported amphibian mass mortality events have been associated with the emerging fungal pathogen *Batrachochytrium dendrobatidis* and viruses of the family Iridoviridae, but other agents such as bacteria, water molds, and trematode parasites have also been associated with varying levels of mortality and population decline.

Chytridiomycosis, an amphibian disease caused by the pathogenic fungus *Batrachochytrium dendrobatidis* (*Bd*), plays a

major role in amphibian population collapses in both protected and disturbed habitats around the world and has been called "perhaps the most virulent threat affecting vertebrates to emerge in recent years" (Hoffman et al., 2010). Catastrophic Bd-related declines have occurred in Central and South America, Spain, Australia, and California (Collins and Crump, 2009). Chytridiomycosis is of great concern in general because it is the first emerging disease that causes declines, and perhaps even extinctions, of many species not otherwise threatened. Scientists debate whether Bd is a novel pathogen, with the spread to new host species and new geographical areas mediated by humans, or an endemic pathogen that has increased in virulence, possibly because amphibians have been rendered more vulnerable by environmental changes. When the fungal load reaches a critical threshold, it fatally compromises electrolyte transport, causing cardiac arrest (Voyles et al., 2009). The ecology of Bd remains poorly understood but we do know that density-dependent host-pathogen dynamics are key components (Briggs et al., 2010; Vredenburg et al., 2010). Many questions remain unanswered: Is reproduction of Bd ever sexual? Are there resting life stages? How is Bd transported?

Viruses belonging to the family Iridoviridae (ranaviruses) have been associated with mass mortality in both frogs and salamanders, in wild populations as well as in captivity. Like *Bd*, spread of these viruses appears to have been at least partly mediated by humans via the global amphibian trade. Ranaviruses appear to have undergone recent host shifts from fish to amphibians.

Other agents contributing to amphibian declines include gram-negative bacterial pathogens; the best-known of these is Aeromonas hydrophila, which causes red-legged disease and has been responsible for local extirpations of wild ranid frogs in California and Rhode Island. Pathogenic water molds (Saprolegnia sp.) have been found to be responsible for local extinctions in some North American frogs, as well as massive egg mortalities in some European frogs, and to increase mortality in at least one North American salamander species. Trematode infestation has been implicated in limb deformities in the Pacific treefrog (Pseudacris regilla) and several other species of amphibians, and to cause tadpole mortality, but so far no major population declines have been tied to trematode infestations. Declines in the Wyoming toad (Bufo baxteri) have been attributed to both Bd and another parasitic fungus, Basidiobolus ranarum.

Human Exploitation

The impact of harvesting wild species for the global pet trade and for human consumption is of increasing concern (Schloegel *et al.*, 2009; Gratwicke *et al.*, 2010). Solutions to these global problems, which often are tied intimately to local economic conditions and traditions, ultimately depend on effective public education.

Factors Associated with Global Climate Change

Amphibians may be more sensitive to climate change than other vertebrates such as birds because amphibians are more likely to show habitat and microhabitat specialization and because they are significantly less vagile. Many of the effects of climate change might be indirect, involving such factors as manifestations of disease or pathogen-host dynamics, and may involve interactions with other stressors (Blaustein *et al.*, 2010), making direct detection of impacts difficult.

Elevated UV-B radiation

Global atmospheric changes caused by anthropogenic activities are well documented and one result is a reduction of stratospheric ozone, leading to an increase in the amount of biologically damaging ultraviolet radiation (UV-B) reaching the Earth's surface. Increase in UV-B has been hypothesized to contribute to increased mortality rates in amphibians with the idea that this might explain enigmatic declines in protected areas. Tests of this hypothesis have focused mainly on comparing egg-hatching rates in species that lay their eggs in shallow, exposed breeding sites that should be subjected to high levels of UV-B. Field experiments have concluded that many species are sensitive, but others are not, even at highelevation sites where the ambient UV-B dose is high. Interactions between UV-B and abiotic factors such as water chemistry are important in some instances. Synergism between UV-B exposure and stress from the risk of predation can increase tadpole mortality in a sensitive species by two-fold over the additive effects of exposure to either stressor alone. Also, not all species that are known to be sensitive to UV-B are in decline. Although UV-B may be involved in synergistic interactions with other factors (Bancroft et al., 2008; Blaustein et al., 2010), at this point it does not appear to be a major component of amphibian declines in general.

Temperature Variability and Amphibian Immunity

Elements of climate change are thought by some to make conditions more favorable for amphibian diseases and parasites (Pounds *et al.*, 2006), but the causal link between climate change and disease virulence is unclear and debated. The rapid spread of *Bd* appears to be sufficient to cause mass amphibian mortalities without invoking climatic change (Lips *et al.*, 2008). However, stress from climate change (in particular, increased temperature variability) may decrease frog immunity, making it easier for pathogens to cause death (Rohr *et al.*, 2008; Rohr and Raffel, 2010).

Threats from Shifts in Weather Patterns

Some species react to changes in climate by shifting their distributions either latitudinally or altitudinally (Rovito *et al.*, 2009). Amphibians, especially those in tropical regions, are narrowly distributed; often they are restricted to specific and narrow elevational belts on mountains that are themselves isolated. There may be no place to go when climates are warm or dry, except higher up the mountain. Species already at the top of such habitats literally are pushed off the mountain, into extinction. Other species may be limited in movements to the north or south by ranges fragmented by habitat conversion or by barriers such as rivers that effectively stop range expansion.

A documented effect of climate change has been the earlier breeding of some species in the northern parts of their ranges. The common frog (*Rana temporaria*) in Great Britain must advance the date of first spawning by three to five weeks in order to accommodate increasing temperatures, but will only be able to advance by five to nine days (Phillimore *et al.*, 2010), so adaptation for this species and other amphibian species may fall well short of the challenge.

In Central America, the cloud line has risen several hundred meters, which apparently precipitated a drought of unusual severity in a high-elevation cloud forest in Costa Rica (Monteverde) in the late 1980s (Pounds *et al.*, 1999). This drought has been implicated in the disappearance of 20 of the 50 species of amphibians known from the site, including a local endemic, the golden toad, *Bufo periglenes*. But it is not clear whether this was the result of an exceptional event (an unusual dry season) or a more general effect, and chytridiomycosis has also been implicated in the disappearance of Monteverde amphibians.

Synergistic Effects

Many factors by themselves pose severe threats to amphibian survival, but synergistic interactions between factors can magnify the negative effects on amphibians. Many different synergistic effects have been suggested, likely posing major threats to the continued existence of numerous amphibian species (Pounds et al., 1999; Relyea and Diecks, 2008; Blaustein et al., 2010). For instance, the effects of infectious diseases may be greater in the presence of unusual weather conditions, elevated UV-B, or chemical pollutants, which may compromise amphibian immune systems. Unusual weather conditions (particularly drought) might enhance the impact of different stressors. The link between climate change and pathogen growth conditions in Central America may be enhanced by the presence of high environmental loads of pesticides in the area, which may be an additional stressor. Hierarchical approaches to defining the causes of declines (Hayes et al., 2010) hold promise for identifying critical factors that might be subjects for further study.

Challenges and Opportunities for the Future

Many of the most dramatic instances of declines have occurred 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 may not ensure survival, but remains an essential strategic component for maintaining ecosystem function. Conservation strategies must involve both specialist and generalist researchers with diverse talents in infectious disease ecology, reproductive biology, endocrinology, immunology, and pollution ecology, as well as knowledge of the natural history of affected species. Ex situ strategies may be essential in particular cases, but captive breeding is difficult and expensive and careful thought must be given to selection of candidate species (e.g., phylogenetic, ecological, and behavioral diversity should be represented). A greater understanding of synergistic effects is required in order to counteract the diverse threats facing this ancient group of organisms.

Mitigation of Habitat Changes

Habitat fragmentation is a cause of declines that might be mitigated by re-establishing habitat corridors and connectivity, such as vegetated freeway overpasses, reforestation, and road tunnels to facilitate wildlife movement.

Wetland restoration holds promise for recovery of some amphibian species. Wetlands are important components of the earth ecosystems, providing vital ecosystem services (i.e., water purification). Mitigation in wetlands not only benefits humans directly by helping restore clean water systems, but also provides important habitat for many species of amphibians.

Removal of Exotic Species

The removal of exotic species has been effective in restoring amphibian populations in some instances. 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 rapid recovery of threatened mountain yellow-legged frog populations. However, whether these population recoveries will translate into species persistence is undetermined; only 1 of 209 amphibian species examined (the Mallorcan midwife toad, *Alytes muletensis*) improved in conservation status due to mitigation of invasive species introductions (Hoffman *et al.*, 2010).

Attenuation of Infectious Agents

Disease ecology seeks to understand the mechanisms that lead to disease outbreaks in natural systems. Global trade, and thus the vast increase in connectivity between continents, has been linked to many of these outbreaks (Schloegel *et al.*, 2009; Gratwicke *et al.*, 2009). Precautions necessary to lower the probabilities of future outbreaks include limiting transport of diseases by use of disinfection and quarantine programs and by stopping human movement of disease vectors (i.e., live bullfrogs). Chytridiomycosis and ranaviral infections are now on the list of notifiable diseases (World Organization for Animal Health, Office International des Epizooties), meaning that all 177 member countries must report on the status of *Bd* and ranaviruses within their borders every six months.

There are a few glimmers of hope for amphibians. Despite the fact that most populations of mountain yellow-legged frogs have been decimated, a few with known infections of *Bd* have persisted for years. Some species of Australian frogs that survived epidemics of chytridiomycosis appear to be re-establishing themselves and to have relatively robust antimicrobial defenses.

Captive Breeding

Although some biologists view captive breeding as a last-resort conservation action, the IUCN endorses captive breeding as a proactive conservation measure, one that should be initiated while a species is still available. IUCN, through its Amphibian Specialist Group, sponsors the Amphibian Ark, which tracks *ex situ* captive breeding activities for amphibians around the world. However, captive breeding is costly and many hurdles

must be overcome (including getting a species to breed successfully in captivity and ensuring that disease is not transmitted) before captive-bred individuals can be reintroduced to the wild (Griffiths and Pavajeau, 2008).

Implications for the Biodiversity Crisis in General

Amphibian declines represent the leading edge of the extinction wave (Wake and Vredenburg, 2008). As humans continue to alter the environment on a global scale, amphibian declines may be the window into the future of what we can expect for global biodiversity: extinctions on a massive scale, well beyond anything we have ever experienced. Despite some local successes, current conservation efforts are insufficient to offset global biodiversity losses. Meanwhile, amphibian declines continue. Although the past decade has seen a dramatic increase in research directed to the multiple and diverse factors associated with declines and significant progress has occurred in many areas, challenges remain. Human activities are a primary source of the problems facing amphibians and, ironically, also the main hope for the future.

See also: Amphibians, Biodiversity of. Captive Breeding and Reintroduction. Captive Breeding and the Evolutionarily Significant Unit. Climate Change and Extinctions. Diseases, Conservation and. Endangered Amphibians. *In Situ, Ex Situ* Conservation. Global Species Richness. Human Impact on Biodiversity, Overview. Indigenous Peoples and Biodiversity. Introduced Species, Impacts and Distribution of. Mass Extinctions, Notable Examples of. Ultraviolet Radiation. Wetland Creation and Restoration. Wetlands Ecosystems

References

- Bancroft B, Baker N, and Blaustein A (2008) A meta-analysis of the effects of ultraviolet B radiation and its synergistic interactions with pH, contaminants, and disease on amphibian survival. *Conservation Biology* 22: 987–996.
- Blaustein AR, Walls SC, Bancroft BA, *et al.* (2010) Direct and indirect effects of climate change on amphibian populations. *Diversity* 2: 281–313.
- Briggs CJ, Knapp RA, and Vredenburg VT (2010) Enzootic and epizootic dynamics of the chytrid fungal pathogen of amphibians. *Proceedings of the National Academy of Sciences USA* 107: 9695–9700.
- Collins JP and Crump ML (2009) *Extinction in our times: Global amphibian declines*. Oxford: Oxford University Press.
- Crawford AJ, Lips KR, and Bermingham E (2010) Epidemic disease decimates amphibian abundance, species diversity, and evolutionary history in the highlands of central Panama. *Proceedings of the National Academy of Sciences* USA 107: 13777–13782.
- Fisher MC, Garner TWJ, and Walker SE (2009) Global emergence of *Batrachochytrium dendrobatidis* and amphibian chytridiomycosis in space, time, and host. *Annual Review of Microbiology* 63: 291–310.
- Gastner MT and Newman MEJ (2004) Diffusion-based method for producing density-equalizing maps. *Proceedings of the National Academy of Sciences USA* 101: 7499–7504.
- Gratwicke B, Evans MJ, Jenkins PT, *et al.* (2010) Is the international frog legs trade a potential vector for deadly amphibian pathogens? *Frontiers in Ecology and the Environment* 8: 438–442.
- Gray MJ, Miller DL, and Hoverman JT (2009) Ecology and pathology of amphibian ranaviruses. *Diseases of Aquatic Organisms* 87: 243–266.
- Griffiths RA and Pavajeau L (2008) Captive breeding, reintroduction, and the conservation of amphibians. *Conservation Biology* 22: 852–861.

- Hayes TB, Falso P, Gallipeau S, *et al.* (2010) The cause of global amphibian declines: a developmental endocrinologist's perspective. *The Journal of Experimental Biology* 213: 921–933.
- Hoffman M, Hilton-Taylor C, Angulo A, et al. (2010) The impact of conservation on the status of the world's vertebrates. Science 330: 1503–1509.
- Lips KR, Diffendorfer J, Mendelson JR III, et al. (2008) Riding the wave: reconciling the roles of disease and climate change in amphibian declines. Public Library of Science Biology 6: 441–454.
- Phillimore AB, Hadfield JD, Jones OR, et al. (2010) Differences in spawning date between populations of common frog reveal local adaptation. Proceedings of the National Academy of Sciences USA 107: 8292–8297.
- Pounds JA, Bustamante MR, Coloma LA, et al. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439: 161–167.
- Pounds JA, Fogden MPL, and Campbell JH (1999) Biological response to climate change on a tropical mountain. *Nature* 398: 611–615.
- Relyea RA and Diecks N (2008) An unforeseen chain of events: lethal effects of pesticides on frogs at sublethal concentrations. *Ecological Applications* 18: 1728–1742.
- Rohr JR and Raffel TR (2010) Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *Proceedings of the National Academy of Sciences USA* 107: 8269–8274.
- Rohr JR, Raffel TR, Romansic JM, et al. (2008) Evaluating the links between climate, disease spread, and amphibian declines. Proceedings of the National Academy of Sciences USA 105: 17436–17441.

- Rovito SM, Parra-Olea G, Vásquez-Almazán CR, et al. (2009) Dramatic declines in neotropical salamander populations are an important part of the global amphibian crisis. Proceedings of the National Academy of Sciences USA 106: 3231–3236.
- Schloegel LM, Picco AM, Kilpatrick AM, et al. (2009) Magnitude of the US trade in amphibians and presence of *Batrachochytrium dendrobatidis* and ranavirus infection in imported North American bullfrogs (*Rana catesbeiana*). *Biological Conservation* 142: 1420–1426.
- Stuart S, Chanson JS, and Cox NA (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306: 1783–1786.
- Stuart S, Hoffmann M, Chanson J, et al. (eds.) (2008) Threatened Amphibians of the World. USA: Lynx Edicions, IUCN, and Conservation International. Spain: Barcelona.
- Voyles J, Young S, Berger L, et al. (2009) Pathogenesis of chytridiomycosis, a cause of catastrophic amphibian declines. Science 326: 582–585.
- Vredenburg VT, Knapp RA, and Tunstall TS (2010) Dynamics of an emerging disease drive large-scale amphibian population extinctions. *Proceedings of the National Academy of Sciences USA* 107: 9689–9694.
- Wake DB and Vredenburg VT (2008) Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences USA* 105: 11466–11473.