

CASE STUDY 3.1

Enigmatic Declines and Disappearances of Amphibian Populations

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The First World Congress of Herpetology in 1989 and a National Research Council workshop in 1990 brought the accelerating losses of amphibian biodiversity to the forefront of conservation concerns. It long had been obvious that habitat destruction and alteration, introduction of nonnative species, pollution, and other human activities exact an increasingly heavy toll upon amphibians as well as on other taxa. By the time of these meetings, however, herpetologists realized that some of the declines and disappearances of amphibian populations and species were unusual in one respect: The causes of their loss were undetermined. These unexplained losses occurred in isolated areas relatively protected from most human impacts, particularly in montane regions in tropical/subtropical Australia, the western United States, Costa Rica, and other parts of Latin America. Especially noteworthy, detailed retrospective studies of declines in amphibians in large national parks in California (Drost and Fellers 1996; Fellers and Drost 1993) and in the Monteverde Cloud Forest Preserve in Costa Rica (Pounds et al., 1997) presented the first conclusive evidence of community-wide declines of amphibians.

Population declines and range contractions have continued. For example, during the latter 1990's 35 of 55 species disappeared from a study area in the Fortuna Forest Reserve in Panama (Lips 1999; Young et al. 2001). However, many of these

cases are complicated by the fact that not all sympatric amphibian species appeared to be affected.

A general problem with these reports was the lack of perspective, with a focus on what may be special cases. To rectify this situation, about 500 amphibian biologists were enlisted to participate in a Global Amphibian Assessment (GAA) conducted from 2000 to 2004 (Stuart et al. 2004). The assessment attempted to evaluate every species of amphibian across the planet, a challenging task when one considers the fact that the vast majority of species are tropical and most of these have been little studied. The GAA documented that the reports were representative of a widespread phenomenon, and that the problem is more acute than generally had been thought; 32.5% of the known species of amphibians are "globally threatened" (Figure A). The assessment also showed that community-wide amphibian declines were more likely to be encountered in the tropics. Many species showed no evidence of declines, however.

The causes of many documented declines and disappearances remain poorly understood despite a burgeoning literature on the subject. Nearly half of the 435 amphibian species classified as rapidly declining by the GAA are threatened primarily by "enigmatic" (unidentified) processes (Stuart et al. 2004). In this case study we briefly review the taxonomic and spatial pat-

terns of these enigmatic losses and their major hypothesized causes. Although the enigmatic declines are our focus, well-documented threats such as habitat loss and overharvesting that are the primary cause of most losses of amphibian biodiversity (including over half of the rapid declines, Stuart et al. 2004) require attention as well.

Although amphibians are more threatened than some other groups, their plight is not unique (Gibbons et al. 2000). The case study of amphibian declines illustrates several themes applicable to studies of biodiversity losses in all taxa:

1. Biodiversity loss has many causes that are not mutually exclusive; several factors may act simultaneously on one population.

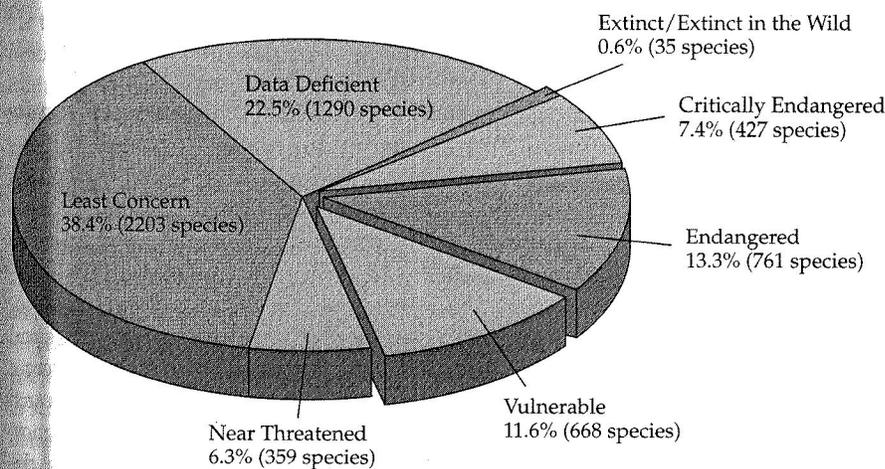


Figure A Over one-third of amphibian species have a threatened designation under the IUCN Red List. (From Global Amphibian Assessment 2004.)

2. Species, and populations within species, vary with respect to the importance of different threats.
3. The combined effect of several stressors can be worse than the sum of their individual effects. These synergistic interactions are especially difficult to study.
4. Experimental demonstration that a factor may affect a population is not proof that it is responsible for observed population declines.
5. No area on Earth is protected from human activities.

Species declining for enigmatic reasons are concentrated in the tropics, especially in Mesoamerica, the northern Andes, Puerto Rico, southern Brazil, and eastern Australia, although the phenomenon may be underestimated in poorly-monitored regions such as Africa (Stuart et al. 2004). Most species (82%) having unexplained declines are frogs and toads in the families Bufonidae, Hylidae, and Leptodactylidae. Ecologically, enigmatic declines are associated with species found in forests, streams, and tropical montane habitats (Stuart et al. 2004). A variety of hypotheses as to the underlying causes of these enigmatic declines have been proposed and studied by a host of conservation scientists.

Ultraviolet-B Radiation

Increased ultraviolet-B (UV-B) radiation is a possible explanation for declines and losses of amphibian populations in comparatively undisturbed areas. A large body of experimental evidence indicates that ambient levels of UV-B are harmful to some amphibian species at some locations, although effects may vary among populations, species, and geographic regions and with ecological factors such as elevation, water chemistry, and the presence of other stressors (reviewed by Blaustein and Kiesecker 2002; Blaustein et al. 2003a). For example, egg mortality in the western toad and Cascades frog was higher when eggs were exposed to ambient levels of sunlight in natural ponds in Oregon than when 100% of UV-B was blocked (Blaustein et al. 1994a; Kiesecker and Blaustein 1995). UV-B had no effect on the survival of Pacific treefrog eggs in the same experiments. The Pacific treefrog was found to have higher levels of an enzyme, photolyase, that facilitates the repair of DNA damaged by UV-B (Blaustein et al. 1994a). Ambient UV-B did not affect survival of western toad eggs in a field experiment conducted in Colorado (Corn 1998). Differences between the Oregon and Colorado results could be due to differences in genes, ecological conditions, or experimental design. UV-B had a greater effect on survival of long-toed salamander larvae from low-elevation populations than those from high-elevation populations under identical conditions in the lab (Belden and Blaustein 2002).

There is also much experimental evidence that UV-B has a greater effect on amphibians when combined with other stressors (Blaustein and Kiesecker 2002; Blaustein et al. 2003a). For example, UV-B decreased the survival of *Rana pipiens* eggs in acidic water but not at near-neutral pH (Long et al. 1995). In

some experiments western toad and Cascades frog eggs died as a result of UV-B increasing their susceptibility to a pathogenic fungus, *Saprolegnia* (Kiesecker and Blaustein 1995; Kiesecker et al. 2001a).

This body of experiments helps us understand some of the impacts of UV-B on amphibians, but does not show that UV-B is responsible for population declines and disappearances. It remains unknown whether the affected populations were exposed to increased UV-B, or that the effects of UV-B extend from individuals to the population level.

Ozone depletion is one factor that may have increased exposure of amphibians to UV-B, even in some locations at low latitudes (Middleton et al. 2001). Many other factors also affect the UV-B dose experienced by amphibians, including the attenuation of UV-B by water and by dissolved organic matter in water, breeding phenology, and behavior (e.g., Corn and Muths 2002, Palen et al. 2002). Climate warming and anthropogenic acidification may reduce concentrations of dissolved organic matter and thereby increase the depth to which UV-B penetrates aquatic habitats (Schindler et al. 1996; Yan et al. 1996).

Ecologists disagree on interpretation of research on the extent to which natural levels of dissolved organic matter currently protect amphibians from harmful levels of UV-B (Blaustein et al. 2004; Palen et al. 2004). Global climate change can affect precipitation, and consequently water depths and UV-B exposure (Kiesecker et al. 2001a). In dry years eggs will be closer to the surface of the water and thus more exposed to UV-B. A complicating factor is that in some regions, such as the Rocky Mountains, montane snow melt and amphibian breeding occur earlier in the season in dry years, when UV-B radiation is lower (Corn and Muths 2002). These issues illustrate why it is difficult to evaluate possible relationships between global climate change and UV-B exposure (Blaustein et al. 2004; Corn and Muths 2004). Integration of information on lethal and sublethal effects of UV-B throughout an amphibian's life cycle with demographic models will bring the phenomenon into a population dynamics framework (Biek et al. 2002; Vonesh and De la Cruz 2002).

Disease Pathogens

Pathogens may cause declines and disappearances of amphibian populations. There was little evidence for this hypothesis until a pathogen new to science, *Batrachochytrium dendrobatidis* (a chytrid fungus), was found in dead and dying frogs collected in the mid-1990's from declining populations in Australia and Panama (Berger et al. 1998; Longcore et al. 1999). *B. dendrobatidis* attacks only tissues that contain keratin, which include the mouthparts in anuran (frog and toad) tadpoles and the skin in salamanders and metamorphosed anurans (Berger et al. 1998; Bradley et al. 2002; Davidson et al. 2003). Research to date suggests that chytrid infections cause little or no mortality of anuran tadpoles or salamanders, although it can decrease the growth rates of the former, making them more susceptible to predators or other stressors (e.g., Davidson et al.

2003; Parris and Beaudoin 2004). *B. dendrobatidis* can kill metamorphosed frogs, either by producing a toxin or by interfering with skin functions such as respiration and osmoregulation (e.g., Berger et al. 1998; Rachowicz and Vredenburg 2004).

Batrachochytrium dendrobatidis has been isolated from other frog populations undergoing mass mortality events associated with population declines and disappearances, including *Rana yavapaiensis*, *R. chiricahuensis*, and *H. arenicolor* in Arizona (Bradley et al. 2002), the midwife toad (*Alytes obstetricans*) in Peñalara Natural Park, Spain (Bosch et al. 2001; Martinez-Solano et al. 2003b), and (retrospectively, using preserved specimens) several species in Las Tablas, Costa Rica (Lips et al. 2003a). It has also been isolated from populations not known to be in decline, including tiger salamanders in Arizona (Davidson et al. 2003), *Litoria wilcoxii* or *jungguy* (taxonomy uncertain) in Australia (Retallick et al. 2004), and *Xenopus laevis* in southern Africa (Weldon et al. 2004). Many individuals in these populations had light infections and appeared healthy. Antimicrobial peptides located in the skin may provide some species with natural defenses against *B. dendrobatidis* (Rollins-Smith et al. 2002a, b). Environmental conditions in some locations may not be favorable for the fungus. For example, *B. dendrobatidis* can grow and reproduce at temperatures of 4°C–25°C, whereas growth ceases at 28°C and 50% mortality occurs at 30°C (Piotrowski et al. 2004). This may explain why amphibian population declines and disappearances associated with chytrids have been observed in cool tropical montane areas (Berger et al. 1998; Lips et al. 2003a), but not in tropical lowlands where temperatures are often above 30°C.

Several scenarios for the association between chytrid fungus infection and population declines and disappearances are possible: (1) amphibians have long coexisted with *B. dendrobatidis*, and observed population changes are cyclical phenomenon that previous researchers may not have noticed; (2) amphibians have long coexisted with *B. dendrobatidis*, but environmental change or stress has made them more susceptible to the fungus or the fungus more pathogenic to the amphibian; and (3) *B. dendrobatidis* is a novel disease recently introduced to susceptible populations around the world through human activities such as the pet trade.

Scenario 1 would follow that of many wildlife diseases, including ranaviruses in North American tiger salamanders and in United Kingdom common frogs (Daszak et al. 2003). This scenario is considered unlikely for amphibian chytridiomycosis because of the large magnitude of the population changes and the lack of recovery in many cases (Daszak et al. 2003).

There are many ways in which an established coexistence between chytrids and amphibians may have changed over time, as in scenario 2. For example, increases in UV-B (Kiesecker and Blaustein 1995), exposure to pesticides (Taylor et al. 1999; Gilbertson et al. 2003), or other stresses can result in immunosuppression and disease emergence. Climate change can induce droughts, causing amphibians to aggregate around water bod-

ies and increasing their exposure to waterborne diseases such as *B. dendrobatidis* (Pounds et al. 1999; Burrowes et al. 2004). Immunosuppression would be likely to increase the prevalence of many diseases, however, not just chytridiomycosis.

Several pieces of data are consistent with the hypothesis that *B. dendrobatidis* is a novel pathogen that has recently been spread around the world with the assistance of humans. For four cases where *B. dendrobatidis* was associated with population declines and disappearances, chytrids could not be detected in museum samples collected prior to the population crash (Berger et al. 1998; Fellers et al. 2001; Lips et al. 2003a). Disease would have to have been very prevalent to allow detection from the small number of samples that were available, however (Lips et al. 2003a). Little genetic variation has been found so far in *B. dendrobatidis* collected around the world, although additional work is needed (Morehouse et al. 2003). Two amphibians that have been transported all over the world, the American bullfrog (*Rana catesbeiana*) and the African clawed frog (*Xenopus laevis*), are carriers of *B. dendrobatidis* (Daszak et al. 2004; Hanselmann et al. 2004; Weldon et al. 2004). The sudden, catastrophic nature of some declines and disappearances also suggests an introduced pathogen (Daszak et al. 2003).

If the chytrid is novel to most areas, where might it have originated? Some workers suggest it is endemic in populations of *Xenopus* in Africa (Weldon et al. 2004). The earliest documented case of chytridiomycosis was in a *X. laevis* collected in South Africa in 1938 (Weldon et al. 2004). The chytrid seems to have a benign relationship to this species, and *X. laevis* is a popular laboratory animal exported worldwide beginning with its use in pregnancy tests in the 1930s.

Introduced Species

Predation and competition from introduced species other than pathogens may have caused declines of some amphibian populations in isolated, seemingly protected areas. For example, the introduction of trout for sport-fishing is thought to have been an important factor in some disappearances of frogs in the Sierra Nevada of California. All but 20 of the 4131 mountain lakes of the state were fishless in the 1830s, as were most high-elevation streams in the Sierra (Knapp 1996). Stocking in Yosemite National Park reached a peak of a million fish each year in the 1930s and 1940s (Drost and Fellers 1996). Stocking has recently been reduced in the Sierra Nevada and discontinued in the region's national parks, in part because of concern about its effects on amphibians (Carey et al. 2003).

The best-documented effects of introduced fishes are for the mountain yellow-legged frog (*Rana muscosa*). It was once a common frog in high-elevation lakes, ponds, and streams of the Sierra Nevada (Grinnell and Storer 1924), but disappeared from over 85% of historical sites in the Sierra (Bradford et al. 1994b; Drost and Fellers 1996; Vredenburg 2004). *Rana muscosa* has a larval period of 1–4 years in the Sierra, and therefore requires permanent bodies of water, as do fishes (Wright and Wright 1949; Knapp and Matthews 2000). There is a strong

negative association between the presence of fish and of *R. muscosa*, even when habitat type and isolation are taken into account (e.g., Bradford 1989; Knapp and Matthews 2000). Densities of *R. muscosa* are low in the few sites where it does co-occur with fishes (Knapp and Matthews 2000; Knapp et al. 2001; Vredenburg 2004). *Rana muscosa* recolonizes lakes from which fishes have disappeared (Knapp et al. 2001) or have been removed experimentally (Vredenburg 2004; Figure B).

Although introduced fishes can account for the disappearance of *R. muscosa* from some sites, *R. muscosa* also disappeared from lakes without fishes in Sequoia, Kings Canyon, and Yosemite National Parks (Bradford 1991; Bradford et al. 1994b; Drost and Fellers 1996). Furthermore, some disappearances occurred during or after the late 1970s, after fish stocking was on the wane. One school of thought is that these other disappearances are an indirect result of fish introductions (Bradford 1991; Bradford et al. 1993; Knapp and Matthews 2000; Vredenburg 2004). According to this hypothesis, *R. muscosa* exists in metapopulations in which populations sometimes go extinct due to natural stochastic processes such as winterkill, drought, disease outbreaks, and predation. Sites are then recolonized by individuals migrating along streams. Stocking of fishes in lakes and streams has reduced the number, size, connectivity, and average habitat quality of *R. muscosa* populations, however. Thus, populations are now more likely to go extinct, and less likely to be recolonized if they do. The time lag between fish stocking and the disappearances of some populations is the

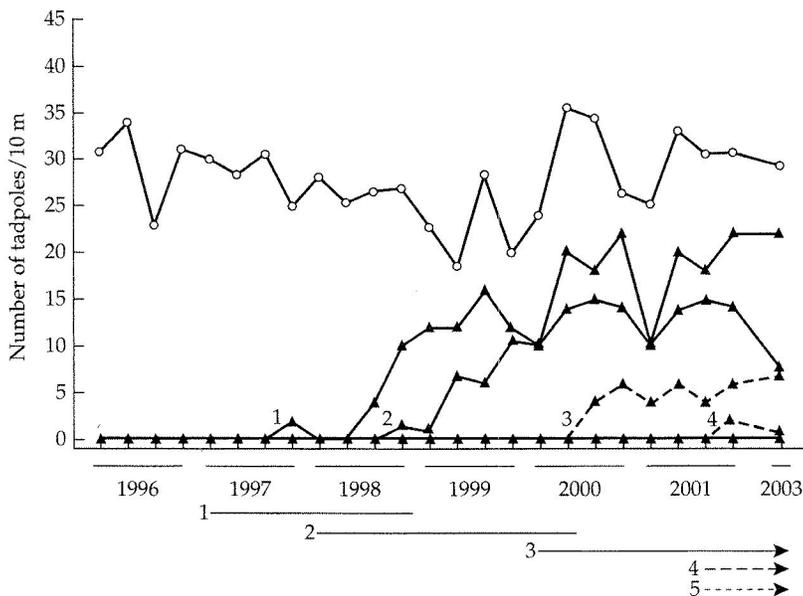


Figure B Density of larval *Rana muscosa* in 21 lakes in the Sierra Nevada, California, from 1996 to 2003. Filled triangles represent trout removal lakes ($n = 5$), and numbers correspond to individual lakes. Open circles indicate fishless control lakes ($n = 8$). The horizontal bars beneath the graph indicate the time period over which trout were removed. *R. muscosa* had not yet recolonized lake 5 after trout were removed in 2001. Control lakes with trout ($n = 8$) never had any frogs present during the duration of the study. No tadpole counts were made in 2002. (Modified from Vredenburg 2004.)

“extinction debt” predicted by metapopulation theory (Hanski 1998; Hanski and Ovaskainen 2002).

Introduced fishes and bullfrogs (*Rana catesbeiana*) are thought to have contributed to widespread range reductions of lowland yellow-legged frogs, *Rana boylei* (Hayes and Jennings 1986; Kupferberg 1997) and red-legged frogs, *Rana aurora* (Adams 2000; Hayes and Jennings 1986; Kiesecker et al. 2001b) in the western U.S. Their role is difficult to evaluate, however, because fish introductions, bullfrog introductions, and habitat alterations have occurred concomitantly across the landscape (Hayes and Jennings 1986). Several experiments have sought to disentangle these factors. Kupferberg (1997) found that bullfrog tadpoles outcompeted *R. boylei* tadpoles, and documented that breeding populations of *R. boylei* were greatly reduced in a stretch of stream that was unaltered except for the presence of *R. catesbeiana*. Experiments with *R. aurora* and native Pacific treefrog (*Pseudacris regilla*) tadpoles concluded that direct effects of the introduced species were less important than the widespread conversion of temporary ponds to permanent ponds, which provide better habitat for the introduced than the native species (Adams 2000). Kiesecker et al. (2001b) found that these habitat alterations intensified competition between *R. aurora* and *R. catesbeiana* tadpoles.

Negative relationships between the distribution of introduced fishes and the distribution and abundance of other amphibians have also been found, including the Pacific treefrog (*Pseudacris regilla*) in the Sierra Nevada (Matthews et al. 2001) and most native species in the mountains of northern Spain (Brana et al. 1996; Martinez-Solano et al. 2003a). The effects of fishes on *P. regilla* and other species are apparently localized, perhaps because they use some habitats that fish cannot, such as ephemeral ponds and terrestrial areas, which may ameliorate landscape-level effects of fish stocking (Bradford 1989; Matthews et al. 2001). *Bufo boreas* and *B. canorus* frequently breed in fishless temporary ponds and produce toxins that fish avoid (Bradford 1989; Drost and Fellers 1996) and these fishes may have little affected their declines. Because fishes have been introduced into nearly all montane systems on the planet, the possibility of impacts exists for many amphibian species, most of which are as yet unstudied.

Chemical Pollutants

Pesticides, herbicides, heavy metals, and other chemical pollutants can have lethal, sublethal, and indirect effects on all organisms, including amphibians (Sparling et al. 2000; Blaustein et al. 2003a; Linder et al. 2003). Chemical pollution might seem to be a minor threat in isolated, protected areas; however, chemical contaminants may be transported long distances through at-

ospheric processes. Further, extremely low, supposedly safe doses of chemicals can harm biota (e.g., Marco et al. 1999; Reylea and Mills 2001). For example, exposure to 0.1 ppb of the herbicide atrazine causes gonadal deformities in northern leopard frogs (*Rana pipiens*) and African clawed frogs (*Xenopus laevis*), whereas the U.S. drinking water standard for atrazine is 3 ppb (Hayes et al. 2003, Hayes 2004).

The best-documented connection between long-distance transport of chemical pollutants and enigmatic changes in amphibian populations is in California. Prevailing winds transport pesticides and other contaminants from areas of intensive agriculture in the Central Valley to national parks, forests, and wilderness areas in the Sierra Nevada (Fellers et al. 2004; LeNoir et al. 1999; Sparling et al. 2001). Disappearances of *Rana aurora draytonii*, *R. boylei*, *R. cascadae*, and *R. muscosa* populations in California are correlated with the amount of agricultural land use and pesticide use upwind (Davidson et al. 2001; Davidson 2004). *Rana muscosa* that were translocated to an area of Sequoia National Park from which they had disappeared (despite the absence of fish) developed higher tissue concentrations of chlor-danes and a DDT metabolite than were found in persisting *R. muscosa* populations 30 km away (Fellers et al. 2004).

These studies provide correlative evidence that pesticides contributed to declines and disappearances of amphibian populations in the Sierra Nevada. Acceptance of this hypothesis will require additional evidence connecting the presence of pesticides and their effects on individuals to effects on populations. This connection cannot be assumed. For example, leopard frogs remain abundant in many areas highly contaminated with atrazine in spite of this herbicide's negative effects on reproductive organs (Hayes et al. 2003). Interactions between pesticides transported long distances and other factors have been suggested as a cause of amphibian declines and disappearances in other protected areas, including Monteverde and Las Tablas, Costa Rica (Pounds and Crump 1994; Lips 1998) and The Reserva Forestal Fortuna, Panama (Lips 1999), but remain little investigated at these sites.

Acid rain is another type of pollution that could affect amphibian populations in isolated areas (Harte and Hoffman

1989). Chemical analyses of water samples in several regions, however, suggested that acid precipitation is an unlikely causal factor (e.g., Richards et al. 1993, Bradford et al. 1994a, Vertucci and Corn 1996).

Natural Population Fluctuations

Population sizes of amphibians, like those of many other taxa, may fluctuate widely due to natural causes. Drought, predation, and other natural factors may even cause local extinctions, necessitating recolonization from other sites. Some declines and disappearances of amphibian populations in areas little affected by humans may be natural occurrences from which the populations may eventually recover, provided that source populations exist elsewhere in the general area (Blaustein et al. 1994b; Pechmann and Wilbur 1994). Natural processes may account for declines and extinctions in the Atlantic forest of Brazil (severe frost and drought, Heyer et al. 1988; Weygoldt 1989), and the loss of some montane populations of the northern leopard frog in Colorado (drought and demographic stochasticity, Corn and Fogleman 1984). Natural fluctuations may also interact with human impacts, resulting in losses from which recovery is unlikely.

Pechmann et al. (1991) used 12 years of census data for amphibians breeding at a pond in South Carolina to illustrate how extreme natural fluctuations may be, and how difficult it can be to distinguish them from declines due to human activities (Figure C). Even "long-term" ecological studies rarely capture the full range of variability in population sizes (Blaustein et al. 1994b; Pechmann and Wilbur 1994). Formulating "null models" of the expected distribution of trends in amphibian populations around the world, against which recent losses may be compared, is a challenging task (see Pechmann 2003 for a review). For example, populations in which juvenile recruitment is more variable than adult survival may decrease more often than they increase, because the average increase is larger than the average decrease (Alford and Richards 1999). The expectation for these populations is that more than half will exhibit a decline over any given time interval even if there is no true overall trend.

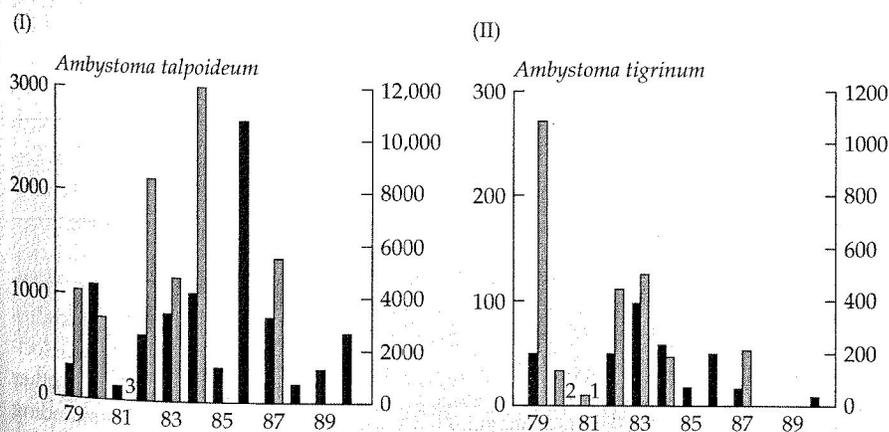


Figure C Natural fluctuations in population size of two species of salamanders in a temporary pond, Rainbow Bay, South Carolina from 1979 to 1990. Numbers of both breeding females (black bars, left axis) and metamorphosing juveniles (gray bars, right axis) vary greatly annually, and some species disappear from and reappear in the system. Numbers in the figure refer to extremely low counts of 3 or fewer individuals. Such species may be poor choices as indicators for the larger system since their natural population fluctuations are so large. (From Pechmann et al. 1991.)

Climate Change

Changes in amphibian population sizes and distributions are often related to changes in environmental temperatures and precipitation (e.g., Bannikov 1948; Bragg 1960; Semlitsch et al. 1996). This variation has traditionally been viewed as natural (Pechmann and Wilbur 1994). The effects of anthropogenic greenhouse gas increases on global climates suggest alternative interpretations in some cases, however.

Some of these alternatives are mediated by the possible effects of greenhouse warming on the El Niño/Southern Oscillation (ENSO), a cyclical warming (El Niño) and cooling (La Niña) of the eastern tropical Pacific. Kiesecker et al. (2001a) found that during El Niño events, precipitation in the Oregon Cascade Mountains was low, resulting in low water levels at *Bufo boreas* breeding sites. The shallow water afforded toad eggs little protection from UV-B radiation, which increased their vulnerability to a pathogenic fungus (*Saprolegnia ferax*), causing high mortality. Kiesecker et al. (2001a) hypothesized that if global warming is increasing the intensity and frequency of El Niño conditions, this may result in amphibian population declines via scenarios analogous to that elucidated by their research with western toads. The effects of global warming on El Niño conditions remain unresolved, however (Cane 2005; Cobb et al. 2003, see Chapter 10).

The disappearance of the golden toad (*Bufo periglenes*) and other frogs from the Monteverde Cloud Forest Preserve in Costa Rica in the late 1980s was associated with an El Niño event, as were subsequent cyclical reductions of some remaining amphibian populations (Pounds et al. 1999). During El Niños, the height at which clouds form increases at Monteverde, reducing the deposition of mist and cloud water that is critical to the cloud forest during the dry season. Pounds et al. (1999) suggested that greenhouse warming has exacerbated this El Niño effect (see Case Study 10.3), citing a global climate model simulation that predicted warming will increase cloud heights at Monteverde during the dry season (Still et al. 1999). This model represents only a crude proxy, because its spatial resolution is too coarse to explicitly model cloud formation on a particular mountain (Lawton et al. 2001; Still et al. 1999). Regional atmospheric simulations and satellite imagery suggest that lowland deforestation upwind also may have increased cloud base heights at Monteverde (Lawton et al. 2001).

Atelopus ignescens and several other *Atelopus* species are thought to have disappeared from the Andes of Ecuador during 1987–1988, which included the most extreme combination of dry and warm conditions in 90 years (Ron et al. 2003). Temperatures in this region increased 2°C over the last century, probably largely due to greenhouse warming (Ron et al. 2003). Other studies also have detected associations between enigmatic declines and disappearances of amphibian populations and temperature and precipitation anomalies (Laurance 1996; Alexander and Eischeid 2001; Burrowes et al. 2004). In these cases the anomalies were within the range of natural variation, thus it is unlikely that they were the direct cause of the amphibian losses, although they may have been a contributing factor. Global

warming has been associated with earlier breeding of some amphibian species (e.g., Beebe 1995; Gibbs and Breisch 2001). Although these phenological changes could potentially result in demographic or distributional changes, there is no evidence that they have to date, except when earlier breeding is associated with dry conditions as for western toads in Oregon (Blaustein et al. 2003b, see also Corn 2003; Kiesecker et al. 2001a).

Subtle Habitat Changes

Subtle habitat changes are an understudied potential cause of enigmatic losses of amphibians. For example, fire suppression in Lassen Volcanic National Park, California, has allowed encroachment of trees and shrubs in and around open meadow ponds, streams, and marshes, rendering these sites unsuitable for *Rana cascadae* breeding (Fellers and Drost 1993). Pond canopy closure is known to have local effects on amphibian biodiversity elsewhere (Halverson et al. 2003; Skelly et al. 1999). Construction of dams in the Sierra Nevada has altered temperatures and hydrological regimes downstream, making the habitat unacceptable for *Rana boylei* breeding (Jennings 1996).

Conclusions

The current thinking of the majority of researchers is that there are many interacting causes for enigmatic amphibian losses. Great challenges face those studying declining amphibian populations in scaling individual effects to the population level. Further challenges include directly testing hypotheses formulated from correlative studies with well-designed field experiments to elucidate those mechanisms that are driving the perceived patterns of decline. Synergistic studies can start by dealing with individual phenomena such as the effects of introduced species, and from this foundation scale up to include multiple factors.

Meanwhile, is there nothing we can do to combat these declines? Not at all. A good example is the rapid rebound of *Rana muscosa* populations following trout removal in the high Sierra Nevada (Vredenburg 2004; see Figure B). Management changes are most likely to be put into effect when direct evidence of the phenomenon has been demonstrated, as has been the case in large national parks in California where fish removal is being actively pursued. Even though fish do not explain all of the declines detected, removal of fishes nonetheless has a salutary effect.

A greater challenge is the infectious disease problem, especially chytridiomycosis. Whereas adult *Rana muscosa* with chytridiomycosis in the laboratory invariably die, field studies have shown that some infected adults can survive the summer (at a minimum) under certain circumstances in the field (Briggs et al. 2005). Models indicate that survival of at least some fraction of infected post-metamorphic individuals is crucial to the persistence of populations (Briggs et al. 2005), and studies in progress should help us understand what factors are associated with survival of infected individuals in this and other species. Achieving a balance between scientific understanding of problems and conservation action is a continuous challenge.

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