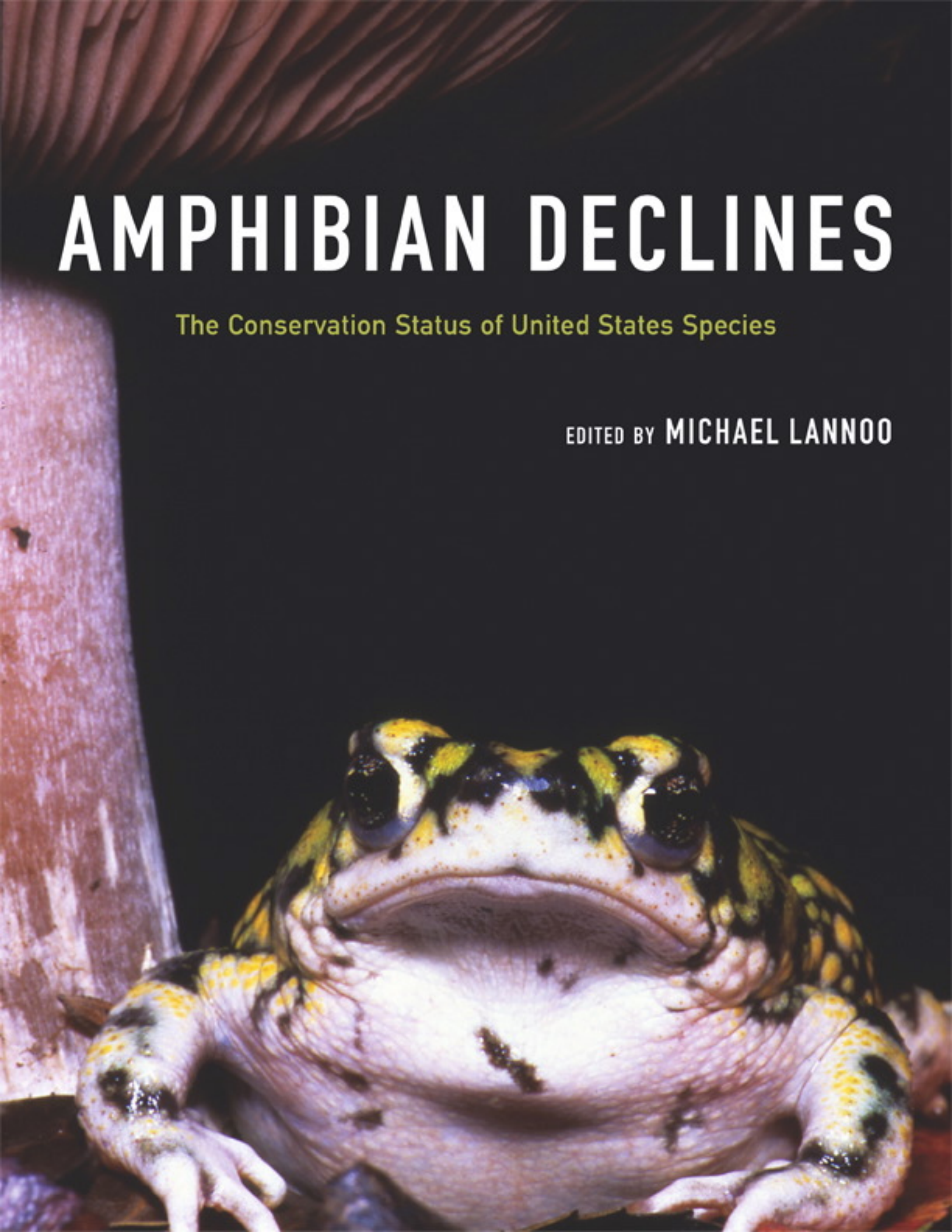
AMPHIBIAN DECLINES

The Conservation Status of United States Species

EDITED BY MICHAEL LANNOO



CAUSES

ELEVEN

Repercussions of Global Change

JAMIE K. REASER AND ANDREW BLAUSTEIN

Living organisms must track the climate regimes appropriate for their survival, adapt to new conditions, or go extinct. In the 1970s, climatologists began to warn that Earth would experience rapid changes, induced in part by emissions of "greenhouse" gases resulting from the burning of fossil fuels, intensifying land use, and reduction in forest cover. They projected that global temperatures would rise substantially in the coming decades (e.g., Climate Resources Board, 1979). At approximately the same time, climatologists also became concerned that chloroflourocarborns (CFCs) and other commonly used industrial gases were depleting the earth's protective ozone layer, thereby increasing the amount of cell damaging ultraviolet B (UV-B) radiation that reaches ground level (van der Leun et al., 1998). Scientists projected that species might concurrently respond to some of these global changes; ranges might shift, natural communities might be disrupted, and mass extinctions of some species might occur (e.g., Peters, 1988).

Amphibians warrant substantial conservation attention. They are considered valuable indicators of environmental quality, and they have multiple functional roles in aquatic and terrestrial ecosystems (Blaustein and Wake, 1990; Stebbins and Cohen 1995; Green, 1997b; Lannoo, 1998b). Furthermore, amphibians provide cultural and economic value to human society (Grenard, 1994; Stebbins and Cohen, 1995; Reaser and Galindo-Leal, 1999; Reaser, 2000a).

As part of the overall "biodiversity crisis," many amphibian populations have been declining and undergoing range reductions (reviewed in Blaustein and Wake, 1995; Stebbins and Cohen, 1995; Reaser, 1996a, 2000a). Indeed, during the past decade, the amphibian decline issue has come to be regarded as an ecological emergency in progress. More than a dozen amphibian species are believed to have recently gone extinct, and the population ranges of many species have been dramatically reduced (Stebbins and Cohen, 1995).

Numerous anthropogenic factors have been implicated as causes of amphibian population declines (see Blaustein and Wake, 1995; Stebbins and Cohen, 1995; Reaser, 1996a, 2000a; Blaustein et al., 2001; Hayes et al., 2002a,c; Kiesecker, 2002; Halliday, this volume; Crump, this volume; Blaustein and Belden, this volume; Bridges and Semlitsch a,b, this volume; Beasley et al., this volume). These factors operate across multiple scales, often have synergistic relationships, and can trigger a cascade of impacts on biological communities. For many such reasons, the site-specific causes of amphibian population declines have been difficult to assess. Habitat destruction and the introduction of invasive alien species (e.g., *Tilapia*, trout) are readily apparent causative agents at some sites, and they present obvious resource management and policy options. However, amphibian population declines in areas with little human activity, especially those in protected reserves, invoke particular concern (e.g., Pounds and Crump, 1994; Lips, 1998, 1999; Pounds et al., 1999). Where amphibians are declining without apparent cause, it is difficult to arrest these declines or to identify what the implications are for the rest of the biological community (including humans).

Recent studies investigating site-specific cases of amphibian declines have revealed that global changes may be involved. Regional warming, increases in ultraviolet radiation, and disease epidemics may all be driven by global phenomena. These global changes might be induced, at least in part, by the increasing intensity and extent of the human impact on climatic and ecological systems.

Global Warming

Severe declines in frog populations at Monteverde Cloud Forest Preserve, Costa Rica, were first noted in 1988 when only eleven golden toads *(Bufo periglenes)* of the 1,500 adults noted the previous year showed up to breed. The last of the species, a single adult male, was observed the following year (Pounds and Crump, 1994; Crump, this volume). Over the following decade, 40% of the amphibian species at Monteverde were decimated in a series of synchronous crashes (Pounds et al., 1999).

The rapid declines in Monteverde occurred during peaks of warm and dry conditions, leading scientists to suspect that the frogs had been physiologically stressed through moisture limitation. Pounds et al. (1999) found that the dry season at Monteverde has indeed become warmer and drier. Furthermore, the dry days are now sustained in longer runs. Pounds et al. hypothesized that the cloud bank in this montane cloud forest has lifted, decreasing misting and condensation. A model produced by a separate team of scientists (Still et al., 1999) to simulate the effects of global warming on tropical montane

cloud forests lends credence to this hypothesis. In addition to amphibian disappearances, populations of two species of lizards disappeared and the ranges of 15 species of birds shifted upslope. The concurrent changes in frog, lizard, and bird populations are all statistically associated with the same regional patterns of mist frequency and congruent with large-scale climate trends.

Pounds et al. (1999) associate the reduction in moisture with the El Niño Southern Oscillation (El Niño) and longer term increases in sea surface temperatures. Globally, average surface air temperatures are about 0.5 °C (almost 1 °F) higher than the average temperatures in the nineteenth century (NOAA, 1997). Analyses by the National Atmospheric and Space Administration (NASA) indicate that the rate of warming is the most rapid of any previous period of equal length in the time of instrumental records (NASA, 1999).

Over a 17-year period in Britain, Beebee (1995) observed a gradual, significant shift in the timing of amphibian breeding. On average, Natterjack toads *(B. calamita)* and edible frogs *(Rana esculenta)* spawned two and three weeks earlier, respectively, in 1990–94, than they did in 1978–82. Three species of European newts *(Triturus vulgaris, T. cristatus,* and *T. heleveticus)* showed highly significant tendencies toward early breeding—by 1990–94, the first newts were arriving 5–7 weeks earlier than in 1978–82. All these shifts in timing of breeding correlate with changes in climate over the same period, with winter and spring average temperatures steadily increasing. In a separate 18-year study, Reading (1998) found that the timing of the arrival of the European toads *(B. bufo)* in south Dorset, United Kingdom, was highly correlated with the mean daily temperatures of the previous 40 days. However, although the five earliest breeding records were within the 10 last years of the study and were associated with particularly mild winters, he did not identify a significant trend toward earlier breeding for this species. In contrast to some of these European data, Blaustein et al. (2001) showed that climate change has not influenced the timing of breeding in at least four species of amphibians in North America for which they had long-term data sets. At one site in Oregon, western toad *(B. boreas)* breeding has been increasingly early and was associated with increasing temperature. However, at four other sites in Oregon, neither western toads nor Cascades frogs *(R. cascadae)* showed statistically significant positive trends toward earlier breeding. At three of these four sites, breeding time was associated with warmer temperatures. In Michigan, spring peepers *(Pseudacris crucifer)* did not show a statistically significant trend to earlier breeding but did show a significant positive relationship between breeding time and temperature. In eastern Canada, Fowler's toads *(B. fowleri)* did not show a trend for earlier breeding nor was there a positive relationship between breeding time and temperature.

While there will undoubtedly be variation in the type, rate, and degree of response amphibian species make to global warming (Ovaska, 1997), it is important to note that observations of amphibian population declines and range shifts attributed to climate change are being reported in other ecological systems. For example, the range of Edith's checkerspot butterfly in Canada, the western United States, and Mexico changed in accordance with a regional climate shift (Parmesan, 1996). Recent events in the marine environment (where just a slight increase in sea water temperature has lead to massive coral bleaching and mortality [up to 90%] in most tropical oceans) are believed to be a large consequence of a steadily rising baseline of marine temperatures (Pomerance et al., 1999; Wilkinson et al., 1999; Reaser et al., 2000a).

Amphibian populations and species most at risk due to global warming are those that (1) are already at the upper limits of their physiological tolerance to temperature and/or dryness; (2) depend on small, ephemeral wetlands; and/or (3) are bound by barriers to dispersal. Because amphibians are reproductively and physiologically dependent on moisture, moisture uptake is temperature sensitive, and amphibian dispersal capacities are low compared with other groups (Blaustein et al., 1994a; Stebbins and Cohen, 1995), it would not be surprising if they are among the first vertebrates to exhibit broad-scale changes in response to global warming.

Ultraviolet Radiation

Many of the amphibian population declines have taken place in remote regions at relatively high elevations, prompting scientists to consider increased ultraviolet irradiance (especially UV-B) associated with depletion of stratospheric ozone as a probable agent. It has also been noted that certain climate changes such as acidification can increase exposure of aquatic organisms to UV-B via effects on dissolved organic carbon, which normally limits UV-B (Schindler et al., 1996).

Several laboratory studies have shown that ultraviolet-B radiation (UV-B; 280–315 nm) can damage amphibians. These studies showed that slightly enhanced UV-B radiation can cause certain deformities in developing frogs and toads (e.g., Worrest and Kimeldorf, 1976; Blaustein et al., 1994c; Anzalone et al., 1998; Blaustein et al., 1998; Corn, 1998; Lizana and Pedraza, 1998; Broomhall et al., 2000; Blaustein and Belden, this volume). Results of field studies strongly indicate that the hatching success of at least nine species of amphibians (from widely separated locales) is reduced under *ambient* UV-B radiation (Blaustein et al., 1998). This includes two frog species, one toad species, two salamander species, and a newt from North America; two frog species from Australia; and a species of toad from Europe. These species comprise a taxonomically diverse group that includes two orders, six families, and seven genera of amphibians. Some of these species are found in montane areas, while others are found at sea level. A key behavioral characteristic shared by these species is that they often lay their eggs in shallow water, where they are exposed to solar radiation.

Hatching success of several other species of frogs in North America and Australia and toads in Europe and North America were not affected by UV-B radiation. Thus, there seems to be differential sensitivity of amphibians to UV-B radiation, perhaps even within a species at different locations. Some of the differential sensitivity may reflect differences in the ability to repair UV-B-induced DNA damage. Those species with the highest levels of the photoreactivating enzyme *photolyase* seem to be the most UV-B resistant species (Blaustein et al., 1998). In addition to studies on the hatching success of embryos, other investigations have shown that ambient levels of UV-B radiation damages eyes in basking frogs (Fite et al., 1998) and causes deformities in developing salamander embryos (Blaustein et al., 1997). Eye damage may impair an individual's ability to avoid predators or find prey, while salamander deformities may affect swimming behavior and cause a number of other problems (Blaustein et al.).

In nature, more than one environmental agent may affect amphibians as they develop. Field experiments have shown that at least three factors may interact synergistically with UV-B: a pathogenic fungus *(Saprolegnia ferax)*, low pH (Long et al., 1995), and fluoranthene, a polycyclic aromatic hydrocarbon

that may pollute aquatic environments impacted by petroleum contamination (reviewed in Blaustein et al., 1998). Thus, these agents in combination with UV-B radiation increase the mortality rates of developing embryos.

UV-B radiation obviously is not the only agent that can contribute to an amphibian population decline. It would be an unlikely factor in the declines of species that lay their eggs under logs, in crevices, in deep water, or under dense forest canopy. Nevertheless, the hatching success of many amphibian species is affected by UV-B radiation. Several factors, such as pathogens, low pH, and pesticides may act synergistically with UV-B radiation to enhance mortality in early life stages. These synergistic interactions may eventually contribute to a population decline.

Infectious Disease

Disease is an important indicator of stress. Recent surges in disease outbreaks throughout a diversity of taxonomic groups and ecological systems (e.g., Epstein et al., 1998; Morell, 1999) have scientists posing the following questions:

1. Is a general decline in environmental quality compromising animal immune systems and making them more susceptible to typically benign microbes (Epstein et al., 1998; Carey et al., 1999)?
2. Are climatic shifts in the environment enabling microbes to increase in virulence, range, and/or diversity (Kennedy, 1998; Daszak et al., 2000; Kiesecker et al., 2001a,c)?
3. Are increases in our technological ability to transport people and products further and faster than at any time in the history of the biosphere facilitating the introduction of microbes to novel environments and hosts (Bright, 1998; Morell, 1999)?
4. Are two or more of these processes concurrently operating to lead to population declines in wildlife (Daszak et al., 1999, 2000)?

A wide diversity of microbes are commonly associated with amphibians (e.g., Gibbs et al., 1966; Carr et al., 1976; Brodkin et al., 1992; Blaustein et al., 1994b). However, larval and adult amphibians whose immune systems have been compromised by acute or chronic stressors may be susceptible to infection by a wide variety of pathogens, and amphibian eggs may become diseased if their gelatinous coating is altered in such a way as to permit the entry of microbes. Scientists investigating declines of amphibians in relatively remote, undisturbed regions have frequently pointed to fungi (e.g., Berger et al., 1998), viruses (e.g., Laurance et al., 1996), or bacteria (e.g., Worthylake and Hovingh, 1989) as the proximal cause of death. Few studies, however, have yet to investigate the potential links between disease outbreaks in amphibians and global change.

Observations and field experiments in Oregon showed that, the pathogenic fungus *Saprolegnia ferax* plays an important role in contributing to the mortality of amphibian eggs in Oregon (Blaustein et al., 1994a; Kiesecker and Blaustein, 1995, 1997b, 1999). Moreover, the fungus interacts with UV-B radiation to enhance mortality in the early life stages of frogs and toads (Kiesecker and Blaustein, 1995). Differential susceptibility of amphibian species to fungus and UV-B radiation may lead to profound changes in community structure (Blaustein and Kiesecker, 1997; Kiesecker and Blaustein, 1999). Recently, Kiesecker et al. (2001a) have shown that there is a complex interaction between climate change, UV radiation, and amphibian susceptibility to *Saprolegnia* infection. Essentially, they suggest that climate-induced reductions in water depth at oviposition sites have caused high mortality of amphibian embryos by increasing their exposure to UV-B radiation and, consequently, their vulnerability to infection.

Fish are intentionally moved from one geographical region to another, even among continents, for a variety of reasons. Fish are also unintentionally relocated. For example, fish are transferred around the world when ships take in ballast water at one location and later release it in another. When fish are introduced to novel environments, their pathogens might also be introduced and thus transmitted to other aquatic species (Bright, 1998), including amphibians. Blaustein et al. (1994c; Kiesecker et al., 2001c) suspect that introducing hatchery-reared fish contributes to the spread of *Saprolegnia ferax* to amphibians. *Saprolegnia*, along with UV-B radiation, seems to be contributing to the decline of the western toad in the Pacific Northwest. Laurance et al. (1996) suggested that a rapidly spreading disease was responsible for the rapid decline of 14 species of endemic, stream-dwelling frogs in the montane rainforests of eastern Australia. They proposed that the pathogen was exotic, brought to the region with aquarium fish, and feared that the thriving international trade in aquarium fish was facilitating the global spread of microbes to which amphibians are susceptible.

We have much to learn about the emergence and spread of amphibian pathogens. Amphibians are themselves traded around the world (Gibbs et al., 1971; Jennings and Hayes, 1985) and are probable vectors when intentionally or unintentionally released into the wild. Because the world trading system is so extensive and complex, controlling trade-mediated epidemics will be a formidable challenge (Bright, 1998). Furthermore, people (including biologists) who come in contact with amphibian pathogens, and thus might transmit them, are increasingly traveling long distances and into remote regions. Every week, about one million people move between the industrial and developing worlds; every day, about two million people cross an international border (Institute of Medicine, 1997).

Conclusion

Because amphibians play multiple functional roles in both aquatic and terrestrial environments, the repercussions of amphibian population declines might be far reaching in time and through space. Profound changes in ecosystems (e.g., Blaustein and Kiesecker, 1997; Kiesecker and Blaustein, 1999) and some socioeconomic systems (e.g., Reaser and Galindo-Leal, 1999; Reaser, 2000a) may occur with a loss of amphibians. Amphibian population declines may become more frequent and severe as temperatures continue to rise, the ozone layer is further depleted, and emerging diseases are rapidly transported around the world.

Clearly, government agencies and other organizations must consider their role in drawing attention to the predicted impacts of global scale perturbations on the resources they manage. Conservation goals can no longer be achieved without taking into account changes in the global system. A comprehensive strategy to maintain amphibian populations must include reducing the emissions of greenhouse and ozone depleting

gases, as well as monitoring and managing their infectious diseases—for even those amphibians granted well-enforced legal protection in refuges, sanctuaries, or parks are threatened by global change. While "thinking globally and acting locally" will reduce some stressors on amphibians, we must now think globally and act globally if we are to conserve amphibians and their habitats.

Summary

Recent studies investigating site-specific cases of amphibian declines have revealed that global changes may be involved. Regional warming, increases in ultraviolet radiation, and disease epidemics may all be driven by global phenomena. These global changes might be induced, at least in part, by the increasing intensity and extent of the human impact on climatic and ecological systems. While there will undoubtedly be variation in the type, rate, and degree of response that amphibian species make to global-scale alterations to the environment, it is clear that amphibian conservation can no longer be achieved without taking into account changes in the global system. A comprehensive strategy to maintain amphibian populations must include reducing the emissions of greenhouse and ozone depleting gases, as well as monitoring and managing their infectious diseases—even those amphibians granted well-enforced legal protection in refuges, sanctuaries, or parks are threatened by global-scale change.