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## ESSAY 5B

### Declines and Disappearances of Amphibian Populations

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The 1990s were rung in with alarm bells concerning declines and disappearances of amphibian populations (Wake and Morowitz 1991). To be sure, much of this news was not new; it has long been obvious that habitat destruction and alteration, introduction of exotic species, pollution, and other human activities have been exacting an increasingly heavy toll upon amphibians as well as other fauna and flora. The problems of frogs, toads, and salamanders, however, had hitherto been relatively neglected. A 1990 National Research Council workshop (Wake and Morowitz 1991) served as a wake-up call concerning the accelerating losses of amphibian biodiversity.

Some of the declines and disappearances of amphibian populations that had occurred since the 1970s were, however, new and unusual in one respect: their causes were unknown. These unexplained losses had taken place in isolated areas relatively protected from most human impacts. For example, the harlequin frog and the only known populations of the golden toad, as well as a number of other species of amphibians, disappeared from the Monteverde Cloud Forest Reserve in Costa Rica during the late 1980s (Crump et al. 1992; Pounds and Crump 1994). Twenty of the 49 species of anurans known to occur in the reserve were still missing in 1996, eight years following the crash (Pounds and Fogden 1996). A number of frogs endemic to the tropical and subtropical montane rainforest streams of eastern Australia disappeared (seven species) or declined (at least four) since the late 1970s, including the gastric-brooding frogs *Rheobatrachus silus* and *R. vitellinus* (Czechura and Ingram 1990; McDonald 1990; Tyler 1991; Ingram and McDonald 1993; Richards et al. 1993). Ranid frogs and bufonid toads suffered a similar fate in many parts of the west-

ern United States, including the areas in and around Sequoia, Kings Canyon, and Yosemite National Parks (Fellers and Drost 1993; Sherman and Morton 1993; Bradford et al. 1994a; Stebbins and Cohen 1995; Drost and Fellers 1996). Diurnal hylodine frogs and other species were reduced or lost in areas of the Atlantic forest of Brazil sampled by Heyer et al. (1988) and Weygoldt (1989). At the El Yunque forest reserve in Puerto Rico, two species of *Eleutherodactylus* became extinct, and five populations of three others apparently disappeared (Joglar and Burrowes 1996). In some of these locations the plot was complicated by the fact that not all sympatric amphibian species appeared to be affected.

Numerous hypotheses have been suggested to explain these puzzling changes in population sizes and distributions, including increased ultraviolet radiation resulting from ozone depletion or other aspects of global change, acid precipitation, pathogens (some perhaps introduced or spread by humans), long-distance transport of chemical pollutants, subtle habitat changes, introduction of nonindigenous species, and natural fluctuations. There is no support for the view that there is a single, global cause; rather, populations probably have declined or disappeared for different reasons. Also, several different factors may have affected any particular population, and the combined effect of several stressors can be worse than the sum of their individual effects.

While discussion of the competing hypotheses has at times been spirited (e.g., Blaustein 1994; Pechmann and Wilbur 1994; Blaustein et al. 1996; Licht 1996), scientific debate is not a sign of disarray. Rather, the questioning and testing of hypotheses is the lifeblood of the scientific method. There is a tension between this process and the need for

conservationists and natural resource managers to reach a consensus and take action before it is too late to save populations and species (Blaustein 1994; McCoy 1994). It is difficult to mount a defense in those cases in which the enemy is unknown, however. If a population decline represents a natural fluctuation, no defense by humans may be necessary. Achieving the proper balance between scientific certainty and conservation action is a continual challenge.

In this essay, we discuss some of the hypotheses that have been proposed to account for the unexplained declines in amphibian populations. The reader should bear in mind that most of the threats to amphibians are well known, and that they threaten other biota as well. The decline and loss of many amphibian populations is beyond doubt, and the main cause—human activities—also seems clear. Knowing this, however, does not tell us in every case what particular dimensions of our activities have caused problems, nor why particular populations are in trouble.

Ultraviolet-B radiation has received much attention as a possible explanation for declines and losses of amphibian populations in comparatively undisturbed areas. The primary evidence for this hypothesis comes from a series of field experiments conducted in Oregon, USA, by Andrew Blaustein and colleagues (Blaustein et al. 1994a; Blaustein et al. 1995; Kiesecker and Blaustein 1995). These experiments demonstrated that egg mortality in the western toad, Cascades frog, and northwestern salamander was higher when the eggs were exposed to ambient levels of sunlight than when 100% of UV-B was blocked. UV-B had no effect on the survival of Pacific treefrog eggs in the same ponds. The Pacific treefrog was found to have higher levels of an

enzyme, photolyase, that facilitates the repair of DNA damaged by UV-B.

The effects of UV-B throughout the life cycle of amphibians, including sublethal effects, should be examined in order to determine whether historical changes in UV-B and factors that influence its impacts are sufficient to have had effects on the population or landscape level. Ozone depletion is one factor that may have increased exposure of amphibians to UV-B, especially at mid- and high latitudes (Stolarski et al. 1992; Herman et al. 1996). Also, climate warming and anthropogenic acidification may have increased the depth to which UV-B penetrates aquatic habitats (Schindler et al. 1996; Yan et al. 1996). Perhaps in some cases UV-B acts primarily to increase the effects of other stressors. Kiesecker and Blaustein (1995) found that the effect of UV-B on western toad and Cascades frog eggs was virtually eliminated when a fungicide was used to remove *Saprolegnia*, a fungus known to kill eggs.

Pathogen infection is another appealing hypothesis that could explain losses of amphibians from many geographic regions. The experiment by Kiesecker and Blaustein (1995) found that *Saprolegnia* increased egg mortality even when the eggs were shielded from UV-B. *Saprolegnia* has been widespread in the environment in Oregon and worldwide for many years, however, so an interaction with some additional stress, such as drought or increased UV-B, must be invoked to explain recent losses (Blaustein et al. 1994b). Another possibility is that the stocking of fish, which carry *Saprolegnia*, has increased the incidence of the disease (Blaustein et al. 1994b).

Redleg (*Aeromonas hydrophila*) is a bacterial disease implicated in the disappearance of the boreal toad (*Bufo boreas*) from the mountains of Colorado (Carey 1993). As is the case for *Saprolegnia*, *Aeromonas* is a ubiquitous, long-established disease that affects fish as well as amphibians. *Aeromonas* is often a secondary infection that strikes animals weakened by natural or anthropogenic stressors. Carey (1993) has hypothesized that some unidentified anthropogenic stress has exacerbated the effects of *Aeromonas* on *B. boreas* in Colorado in recent years. Laurance et al. (1996) have hypothesized that an exotic epidemic disease, perhaps an iridovirus, is responsible for the catastrophic declines of Australian rainforest frogs. They have hypothesized

further that human activities, such as the international trade in aquarium fishes, introduced the disease to Australia and elsewhere. Although some characteristics of the Australian declines are consistent with the disease hypothesis, they are also consistent with other hypotheses.

Acid precipitation has probably had negative effects on some amphibian populations, such as natterjack toads at heathland sites in Britain (Beebee et al. 1990). Experiments conducted by Harte and Hoffman (1989) on a Rocky Mountain population of tiger salamanders suggested that episodic acidification associated with the release of contaminants into breeding ponds during snowmelt resulted in deformities and mortality of embryos, and consequently a decline in population size during the mid-1980s. Wissinger and Whiteman (1992) documented a rebound in numbers in this population beginning in the late 1980s. They found that during their study, the salamanders either bred after the spring acidity pulse or the pulse was benign, and suggested that the 1980s decline may have been related to pond drying. Chemical analyses of water samples suggested that anthropogenic acid precipitation is an unlikely explanation for declines and disappearances of amphibians in other parts of the Rocky Mountains (Corn and Vertucci 1992; Vertucci and Corn 1996), the Sierra Nevada (Bradford et al. 1994b), the tropical rainforest of Australia (Richards et al. 1993), and the Monteverde Cloud Forest Reserve in Costa Rica (Crump et al. 1992). Additional data on within-year variation and long-term trends in acidity at breeding sites in these regions, and on the sublethal effects of acidity on species of concern, are necessary for definitive evaluation of the acid precipitation hypothesis.

Predation and competition from introduced species may have been responsible for the declines of some amphibians. The American bullfrog was introduced in California before the turn of the 20th century and has long been implicated in the disappearance of the red-legged frog from much of its range in the Central Valley and the Sierra Nevada foothills (Moyle 1973; Hayes and Jennings 1986). Its effect on populations of the lowland yellow-legged frog in northwestern California has been documented recently (Kupferberg 1996). The introduction of trout for sport-fishing is thought to have been an important factor in the disappearance of

Sierra Nevada frogs (Hayes and Jennings 1986; Bradford 1989). All but 20 of the 4131 mountain lakes of the state were fishless in the 1830s (Knapp 1996). Stocking of lakes in Yosemite National Park reached a million fish each year in the 1930s and 1940s, and may have gradually reduced the number of permanent source lakes that harbored base populations of frogs. Thus as frogs gradually disappeared from small, semi-isolated lakes as a result of predation or drought, chances of recolonization became steadily reduced. Declines of amphibians were most dramatic many years after the most intense stocking activity, so it is unlikely that introduced fish are the main culprit (Drost and Fellers 1996).

Chemical pollutants that were previously undetected or whose effects have been underestimated represent another possible explanation for declines and disappearances of amphibians in areas that appear to be relatively undisturbed (Berrill et al. 1993; Stebbins and Cohen 1995). For example, atmospheric transport of pesticides from California's Central Valley to the Sierra Nevada has recently been documented (Zabik and Seiber 1993). Researchers have now begun to realize that extremely low doses of pesticides and other synthetic chemicals, especially mixtures of them, may mimic, block, or disrupt natural hormones (Stebbins and Cohen 1995; Arnold et al. 1996); these substances may affect embryonic development as well as adult reproduction (Guillette et al. 1995). Thus, levels of synthetic compounds that were previously considered "safe" for wildlife may have significant effects on populations.

Population sizes of amphibians, like those of other groups, may fluctuate widely due to natural causes. Drought, predation, and other natural factors may cause local populations to go extinct, 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 on their own, provided that source populations exist elsewhere in the general area (Blaustein et al. 1994c; Pechmann and Wilbur 1994). Natural processes have been hypothesized to account for the losses of the golden toad and harlequin frog (drought, Crump et al. 1992; Pounds and Crump 1994), 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 influences, resulting in losses from which recovery may be unlikely. For example, Bradford (1991) and Bradford et al. (1993) hypothesized that natural processes had eliminated some populations of the mountain yellow-legged frog, but that stocking of predatory fish in streams used by the frogs as dispersal corridors prevents recolonization of these sites.

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 (see Figure 12.5; see also Semlitsch et al. 1996 for an update and data for additional species). Even "long-term" ecological studies rarely capture the full range of variability in population sizes (Pechmann and Wilbur 1994; Blaustein et al. 1994c), because the observed variation may continue to increase over time (even after 100 years for some insects, Hanski 1990). Several authors have argued that the unexplained declines and disappearances they have observed in amphibian populations over the last 20 years are too extreme, too widespread, or too long-lasting to be natural fluctuations (e.g., Drost and Fellers 1996; Laurance et al. 1996). However, inadequate data exist

at present to formulate a "null model" of the expected distribution of trends in amphibian populations around the world, against which recent losses could be compared (Blaustein et al. 1994c; Pechmann and Wilbur 1994; Travis 1994).

Numerous documented declines and disappearances of amphibian populations remain unexplained, although many hypotheses have been proposed. The current thinking of the majority of researchers is that there are probably many interacting causes for these losses. Perhaps the only certainty is that *Homo sapiens* is a major culprit in the biodiversity crisis affecting amphibians and other taxa.