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SETAC Technical Publications Series

Current Coordinating Editor of SETAC Books
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Publication sponsored by the Society of Environmental Toxicology and Chemistry

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2000

CHAPTER 12

Publication #424

Amphibian Declines: Review of Some
Current Hypotheses

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Declines of varying severity in the size of amphibian populations have been observed for many years (Bragg 1960; Gibbs et al. 1971; Cooke 1972; Beebe 1973; Bury et al. 1980; Andren and Nilson 1981; Hamner 1982; Corn and Fogelman 1984; Hayes and Jennings 1986; Heyer et al. 1988), but concern among conservation biologists increased dramatically after the First World Congress of Herpetology in 1989 at Canterbury, UK. Several papers and posters at that meeting presented evidence of recent declines, and discussions among the attendees heightened concern about the status of amphibians globally. Continuing dialogue led to a workshop in February 1990 at Irvine, California, sponsored by the National Research Council Board on Biology. The consensus of the participants of that meeting was that amphibian population declines were real but documentation was largely anecdotal, and much work was needed on the causes of population declines (Barinaga 1990; Blaustein and Wake 1990). The Irvine meeting received considerable media attention, with reporters from print media and *National Public Radio* in attendance. The initial coverage of the problem (e.g., Booth 1989; Tugend 1990) even caught the attention of the supermarket tabloids (Stern 1990), and the problem of disappearing frogs occupied agents Scully and Mulder in one episode of the television show *The X-Files* (Newton 1996). Relying on amphibians' usual status as uncharismatic microfauna, public interest in these animals and their status remains high, sustained by continuing, more serious coverage in the popular media (e.g., Yoffe 1992; Quammen 1993; Argo 1996; Luoma 1997).

Some of the goals of the Irvine meeting have been met. The last eight years have seen considerable progress in documentation of status and current distributions of amphibians (e.g., Kuzmin et al. 1995; Pyke and Osborne 1996; Green 1997a; Lannoo 1998b), increased communication among researchers through the World Conservation Union Declining Amphibian Populations Task Force and its newsletter, *Froglog*, and further research into causes of declines. The latter has proven to be the most problematic. Amphibians are not the only vertebrates with evidence of recent declines, but in other groups such as birds (Terborgh 1989; Root and Weckstein 1994) or native fishes in western North America (Minckley and Deacon

Aldo Leopold Wilderness Research Institute: Publication # 424

CITATION: Corn, Paul Stephen. 2000. Amphibian Declines: Review of Some Current Hypotheses. In: Sparling, Donald W.; Linder, Greg; Bishop, Christine A., eds. Ecotoxicology of Amphibians and Reptiles. Columbia, MO: U.S. Geological Survey, Midwest Science Center: 663-696.

1991; Frissell 1993; Rinne and Janisch 1995), anthropogenic changes in habitat (including introduction of non-native predators) are considered to be responsible for the population declines. Habitat alteration and destruction are probably also the causes of many amphibian population declines (Corn 1994; Blaustein and Wake 1995; Stebbins and Cohen 1995), but a variety of other factors, both anthropogenic and natural, have been observed or proposed as causes of declines in size or extinctions of amphibian populations. Unfortunately, determining the causes of population declines of many species has proven difficult (Sarkar 1996). This is frustrating to students and particularly when confronted with the inevitable question, often from a reporter, *Why?* However, before examining the current knowledge of the causes of amphibian declines, a review of the status of amphibian species and populations is necessary.

Overview of Amphibian Declines

There has been some controversy over what is meant, exactly, by the term "declining amphibian populations" (see Blaustein 1994; McCoy 1994; Pechmann and Willbur 1994). Green (1997b) provided a convenient framework, distinguishing between declines in size of populations and declines in numbers of populations. Concern over population size is certainly justified in specific cases (e.g., endangered species), but population studies are fraught with many complexities, including effects of the complex life cycles of amphibians, influences from external variables such as weather, and even the ability to accurately estimate population size. The inherent variability in size of populations of pond-breeding amphibians requires long-term data to establish trends. Several studies of amphibian abundance at one or a few locations recorded declines in population size, sometimes lasting for several years, followed by increases in abundance back to or greater than the population size before the decline began (Pechmann et al. 1991; Semlitsch et al. 1996; Green 1997c; Meyer et al. 1998; P.S. Corn, unpublished data). Moreover, a decline in the size of one population may be meaningless in the larger context of the metapopulation, and monitoring sizes of multiple populations is, at best, impractical. Green (1997b, p 293) proposed a more useful definition:

A decline is the condition whereby the local loss of populations across the normal range of a species so exceeds the rate at which populations may be established, or reestablished, that there is a definite downward trend in population number.

The boreal toad (*Bufo boreas boreas*) in the southern Rocky Mountains illustrates the loss of populations (Figure 12-1). Green included several caveats to restrict the application of the term, including "rarity alone does not equal decline," "population fluctuations are not declines," "local habitat destruction does not signify permanent population loss," and "current absence does not imply former presence." In this

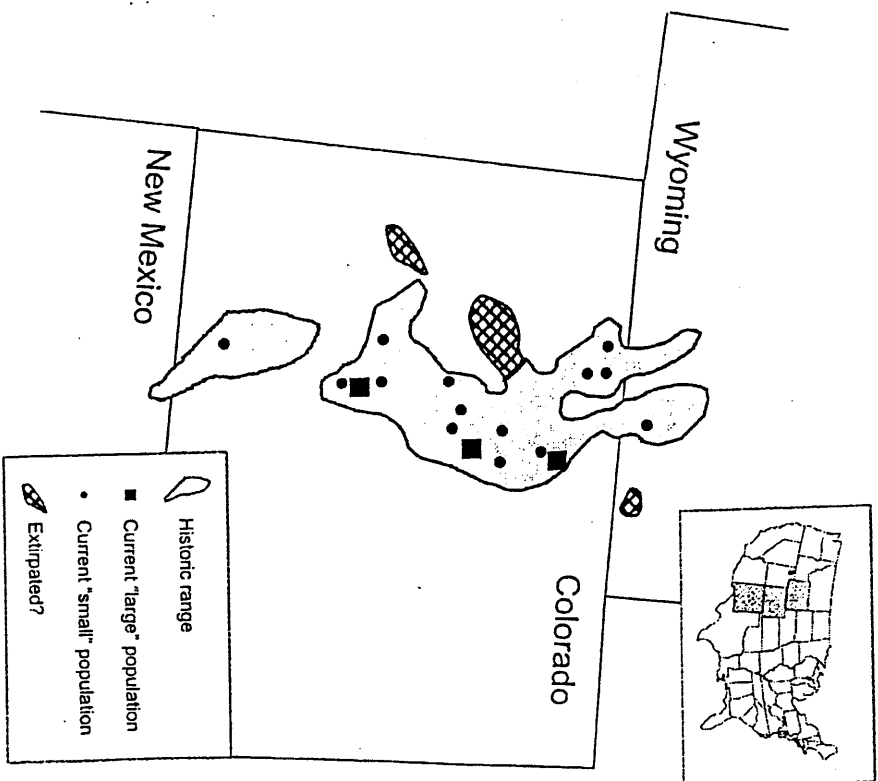


Figure 12-1 Distribution of the boreal toad (*Bufo boreas*) in the southern Rocky Mountains (after Hammerson 1999, Loeffler 1998). Large populations encompass one or more localities with > 10 clutches produced annually. Small populations produce < 5 clutches each year.

review, I will provide the greatest detail on the situations with which I am most familiar (western North America), although I will review published accounts of amphibian declines elsewhere in the world. I have attempted to apply Green's definition to the published accounts of amphibian declines. However, this has proven difficult for two reasons. First, relatively few status surveys have encompassed areas large enough that population loss could be proven. Many accounts of population declines still involve a restricted number of sites. Second, many published accounts still provide anecdotal rather than quantitative data. Therefore, I have probably listed declines of some species that do not fit Green's definition.

Declines in temperate North America

Amphibian declines have been studied extensively in North America, especially in the West (Corn 1994; Stebbins and Cohen 1995). The volume of information on the status of amphibians in eastern North America is increasing rapidly (Green 1997a, Lannoo 1998b). There are now 16 species of amphibians in the U.S. and its territories listed as threatened (7 species) or endangered (9 species) (USFWS 1998b). Most of these species have been on the list since the 1980s and represent narrowly distributed endemics threatened by habitat destruction (Bury et al. 1980). Species with these traits do not exemplify the recent problem of amphibian population declines; i.e., the growing number of widely distributed, formerly common species that have declined (Bury et al. 1995).

However, not all endangered endemic species are threatened by habitat destruction. The Wyoming toad (*Bufo hemiophrys baxteri*), a glacial relict restricted to the Laramie Basin in southeast Wyoming (Baxter et al. 1982), has declined to the point at which it is maintained only by intensive captive breeding (Corn 1994). Habitat destruction does not appear to be an important factor in this decline. In fact, irrigation and water storage have probably increased available habitat for Wyoming toads in the past 100 years. The proximate cause of the extinction of the last known wild population of this species was apparently disease—mycotic dermatitis caused by the asprophytic fungus *Basidiobolus* sp. (Taylor et al. 1995). However, we do not know if this represents a novel pathogen or if the ultimate cause is something else. Other stresses may have reduced the effectiveness of the immune system, leading to increased susceptibility of toads to fungal infection (Carey 1993). We also do not know if the fungus was responsible for the range-wide decline of the Wyoming toad in the 1970s and early 1980s, or if the problem was restricted to the one population studied since 1987. This illustrates some of the main problems in trying to determine causes of amphibian declines: lack of evidence and the impossibility of conducting experiments on populations that no longer exist.

Extensive population declines transcend the paradigm of endemic species threatened by habitat destruction. Declines in occurrence of species with larger distributions have entered the consciousness of management agencies, as evidenced by the recent listing of the California red-legged frog (*Rana aurora draytonii*) as threatened (USFWS 1996) and the arroyo toad (*Bufo californicus*) as endangered (USFWS 1994), as well as the petitions to governments to list the boreal toad and the spotted frog (*Rana pretiosa* complex). The California red-legged frog and arroyo toad have lost about 75% of known populations (Jennings 1995; Stebbins and Cohen 1995). The arroyo toad is a riparian species that has been seriously affected by water impoundments and intensive human recreation (off-road vehicles, fishing, gold dredging) within its restricted habitat (USFWS 1994; Stebbins and Cohen 1995). A variety of problems beset the California red-legged frog, including habitat destruction by urbanization and agricultural development, introduced predators, historical over-exploitation by humans as a food source, and possibly agricultural pesticides

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(Jennings and Hayes 1984, 1994; Hayes and Jennings 1986; Fisher and Shaffer 1996).

Many other species have declined in California and the southwestern U.S. Populations of the Santa Cruz long-toed salamander (*Ambystoma macrodactylum croceum*), California tiger salamander (*A. californiense*), and Sonoran tiger salamander (*A. tigrinum stebbinsi*) have been lost, and declines in abundance within populations have occurred (Collins et al. 1988; Ruth 1988; Barry and Shaffer 1994; Fisher and Shaffer 1996). The Santa Cruz long-toed salamander was included with the first group of species listed as endangered in 1967 (USFWS 1998b), and declines of Sonoran tiger salamanders in Arizona and Sonora led to its recent listing as endangered (USFWS 1997). Declines of western toads (*B. boreas*) and Yosemite toads (*B. canorus*) have occurred in the Central Valley and Sierra Nevada in California (Kagarise Sherman and Morton 1993; Drost and Fellers 1996; Fisher and Shaffer 1996). Ranid frogs, as a group, appear to have experienced the most extensive population declines. Besides the California red-legged frog, population loss has been documented in California for the foothill yellow-legged frog (*R. boylei*), Cascades frog (*R. cascadae*), Oregon spotted frog (*R. pretiosa*), mountain yellow-legged frog (*R. muscosa*), northern leopard frog (*R. pipiens*), and Yavapai leopard frog (*R. yavapaiensis*) (Moyle 1973; Bradford 1983, 1989, 1991; Hayes and Jennings 1986; Jennings 1988, 1995, 1996; Fellers and Drost 1993; Jennings and Hayes 1994; Drost and Fellers 1996; Fisher and Shaffer 1996; Knapp 1996). Among native species, only the northern red-legged frog (*R. a. aurora*) has a relatively stable population (Jennings 1995), although its abundance is reduced in Oregon's Willamette Valley (Blaustein and Wake 1995). Two introduced species, the bullfrog (*R. catesbeiana*) and Rio Grande leopard frog (*R. berlandieri*), have expanding distributions (Moyle 1973; Hayes and Jennings 1986; Platz et al. 1990; Jennings and Hayes 1994).

The status of ranid frogs in Arizona and New Mexico is similarly dismal. The Tarahumara frog (*R. tarahumarae*) apparently has been extirpated from the U.S. at the northern margin of its range (Hale et al. 1995). Other native leopard frogs, including the plains (*R. blairi*), Chiricahua (*R. chiricahuensis*), northern, and Yavapai are missing from 60 to 90% of known localities (Clarkson and Rorabaugh 1989; Stredl and Howland 1995; Degenhardt et al. 1996; Stredl, Howland et al. 1997). The recently described Ramsey Canyon leopard frog (*R. subaquavocalis*) is an apparent exception to this trend (Stredl, Howland et al. 1997). Non-native predators, including crayfish, fishes, bullfrogs, and possibly Rio Grande leopard frogs appear to be the primary agents in the decline of Arizona's native frogs (Rosen et al. 1995; Stredl, Howland et al. 1997), but habitat destruction, disease, and extreme weather events (flash flooding in streams and drying of cattle tanks) have affected individual populations (Stredl, Collins et al. 1997).

Declines in populations elsewhere in North America usually do not include most of a region's species as is the case in California and Arizona, but severe declines of historically abundant and widely distributed species have been documented. Corn

et al. (1989) documented the absence of boreal toads from more than 80% of known localities in northern Colorado and southern Wyoming. Carey (1993) documented the extinction of 11 populations of that toad in central Colorado in the 1970s and 1980s. The boreal toad apparently is extirpated from the few known locations in New Mexico (Stuart and Painter 1994) and from two or three other areas: the Grand Mesa and White River Plateau in Colorado and the Pole Mountains in Wyoming (Figure 12-1). Recent surveys have located 34 sites in Colorado in which boreal toads currently breed (Loeffler 1998), but most of these represent small populations with fewer than five breeding pairs. Boreal toads are now rare in the mountains of Utah and in and around Yellowstone and Grand Teton National Parks in Wyoming and Idaho (Koch and Peterson 1995; Ross et al. 1995). In some Oregon populations of boreal toads, Olson (1992) described declines in abundance of adult toads and Blaustein, Hokit et al. (1994) described mortality of several million eggs. But there is no published evidence that boreal toad populations have been lost and declined in the mountains of the Pacific Northwest to the extent reported in the Rocky Mountains. Indeed, toads have recovered rapidly from the 1980 eruption of Mount St. Helens in southern Washington and are now abundant within the blast zone, where the forest was leveled and buried in a meter of ash (Crisafulli and Hawkins 1998; P. S. Corn, personal observation). However, boreal toads are apparently rare at lower elevations, particularly in the Puget Sound lowlands of Washington. Three recent surveys found this species present at 0 to 22% of sites surveyed (Richter and Azous 1995; Adams et al. 1998, 1999).

Carey (1993) observed boreal toads with symptoms of red-leg disease (*Aeromonas* bacterial infection) and hypothesized that this was the proximate result of stress that had weakened the toads' immune system. This is difficult to evaluate because the stressor is not readily apparent and excessive mortality has not been observed recently in toads in the Rocky Mountains. Blaustein, Hokit et al. (1994) attributed egg mortality to the fungus *Saprolegnia*. Olson (1989) observed predation by ravens (*Corvus corax*) on adult toads. However, predation by native predators is unlikely to have caused the widespread decline in occurrence of the boreal toad, although it may have serious consequences for small populations of toads (Corn 1993).

Declines in populations of northern leopard frogs in the Midwestern U.S. were among the first reported for a widely distributed, abundant species (Gibbs et al. 1971; McKinnell et al. 1979; Hine et al. 1981). Besides Arizona and California, declines of western populations have been observed in British Columbia, Colorado, Manitoba, western Montana, Saskatchewan, Washington, and the Yellowstone region (Hammerson 1982; Corn and Fogleman 1984; Corn et al. 1989, 1997; Koonz 1992; Orchard 1992; Roberts 1992; Seburn 1992; Koch and Peterson 1995; Reichel and Flath 1995; Leonard and McAllister 1996; Wagner 1997; Weller and Green 1997). The northern leopard frog is almost extirpated from British Columbia, and in April 1998, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) declared this species endangered in British Columbia and vulnerable in

Alberta (David M. Green, McGill University, personal communication). In the prairies of central North America, the severe declines in amphibian population size and occurrence of the 1960s and 1970s do not appear to be occurring now, with the exception of eastern Alberta. Recent surveys for leopard frogs revealed stable, slightly declining, or increasing populations (Didiuk 1997; Weller and Green 1997; Moriarty 1998; Mossman et al. 1998). Populations of leopard frogs in eastern North America have not undergone the declines observed in the Midwest and West (McAlpine 1997; Weller and Green 1997; Orr et al. 1998). Various causes have been listed for declines of northern leopard frogs, including drought, predation by bullfrogs, and red-leg disease (Hammerson 1982; Corn and Fogleman 1984; Orchard 1992; Koonz 1992). A significant commercial harvest on leopard frogs has also existed (Gibbs et al. 1971; McKinnell et al. 1979; Koonz 1992; Lannoo et al. 1994), but most authors have concluded that reduced harvests observed in the 1970s were a consequence of the decline and not the cause. Lannoo et al. (1994) pointed out that the decline of northern leopard frogs in northwestern Iowa, from an estimated minimum of 20 million individuals in 1900 to about 50,000 in 1992, parallels the 90 to 98% loss of wetlands during the same period.

The decline of the Oregon spotted frog in the Pacific Northwest is probably the most severe of any widely distributed species in North America. The magnitude of the decline is under-appreciated because this species was only recently differentiated from the more common Columbia spotted frog, *R. lateralis* (Green et al. 1997). Oregon spotted frogs historically occurred in the Cascade Mountains of Oregon and northeastern California, the Willamette Valley in western Oregon, and the Puget Trough of western Washington and southwest British Columbia (Figure 12-2). This species apparently has been absent from the Willamette Valley for several decades (Dumas 1966; Nussbaum et al. 1983). A single population was recently discovered in British Columbia (Weller and Green 1997), and three populations currently exist in Washington (McAllister et al. 1993; McAllister and Leonard 1997). A few populations are still known to occur in the Oregon Cascades (Hayes 1997, cited in McAllister and Leonard 1997). Dumas (1966) hypothesized that introduced bullfrogs were responsible for the decline of Oregon spotted frogs. McAllister and Leonard (1997) listed introduced predators (warm-water fishes) and wetland drainage as the most likely causes of the decline in Washington.

Declines in occurrence and sizes of populations of Columbia spotted frogs have been documented in Nevada and along the west slope of the Wasatch Mountains in Utah (Turner 1962; Ross et al. 1993; Reaser 1996). However, this frog is still common throughout most of the rest of its range in the northern Rocky Mountains, where it is usually the most abundant amphibian (Koch and Peterson 1995; Reichel and Flath 1995; Munger et al. 1996; Mennell 1997; Weller and Green 1997).

Declines in occurrence and population size at the southern end of its range are attributed to changing water use, grazing, and urbanization (Turner 1962; Ross et al. 1993; Reaser 1996), but long-term climate change has been acting to isolate these

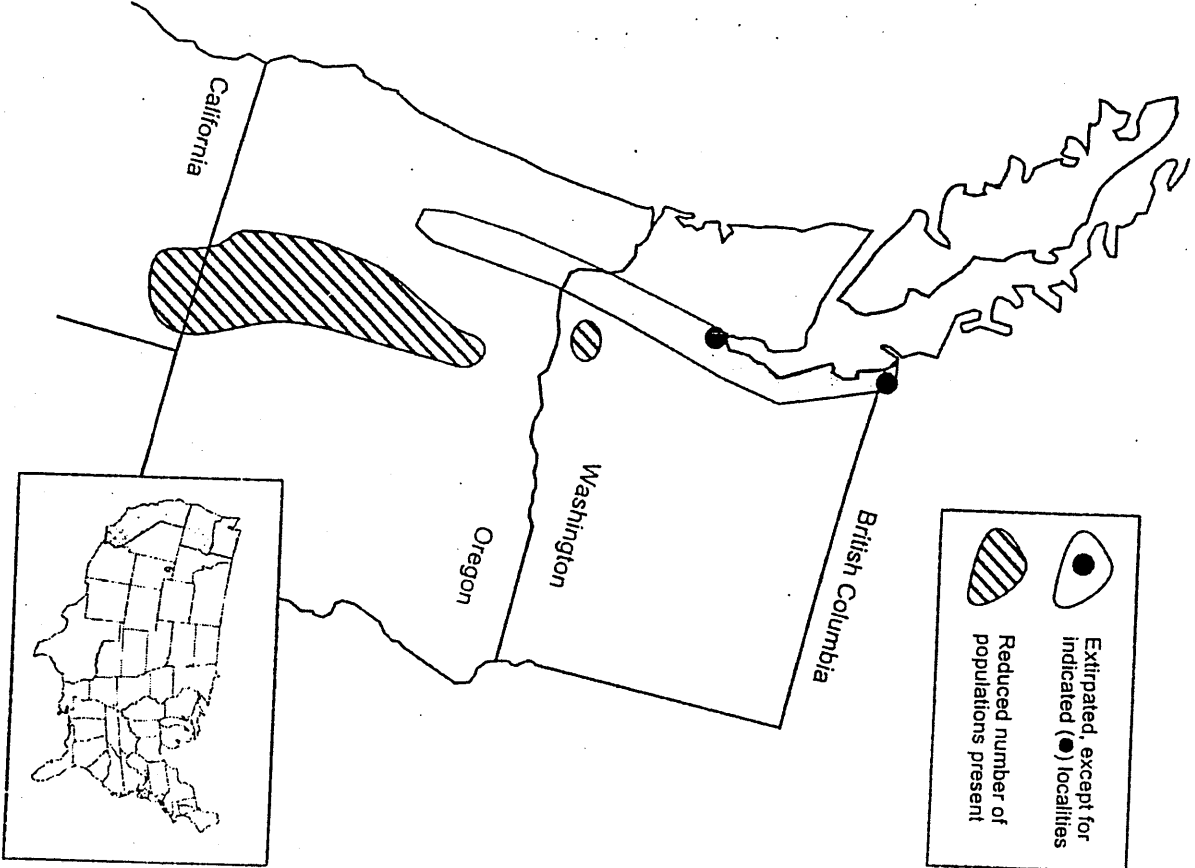


Figure 12-2 Distribution of the Oregon spotted frog, *Rana prairiata* (after McAllister and Leonard 1997)

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populations since the end of the Pleistocene (Green et al. 1996). Utah populations of Columbia spotted frogs are the objects of a Conservation Agreement between the State of Utah and the U.S. Fish and Wildlife Service (USFWS 1998a).

Further east, the geographic range of the cricket frog (*Acris crepitans*) is going the opposite direction—retreating from the northern margin of its range (Lannoo et al. 1994; Casper 1998; Hay 1998; Lannoo 1998a). It apparently is extirpated from its only known locality in Canada and is listed as endangered by COSEWIC (Weller and Green 1997). This species was listed as abundant in six parks in Hamilton County in southwest Ohio and was not considered to be declining in occurrence (Davis et al. 1998). Causes of the decrease in cricket frog populations have not been discovered, but climate and agricultural practices have been suggested as possibilities (Hay 1998). Lannoo (1998a) suggested that a combination of drought and conversion of permanent wetlands to recreational fisheries has severely reduced habitat for this species in the upper Midwest.

Except for the cricket frog, few declines of common, widely distributed species have been documented in eastern North America (Weller and Green 1997). The hellbender (*Cryptobranchus alleganiensis*), a large aquatic salamander, is listed as endangered by several Midwestern states (Levell 1995), but relatively little is known about population trends of this secretive species (Pfungsten 1990). The flatwoods salamander (*Ambystoma cingulatum*) is not especially common, but it is broadly distributed on the southeastern coastal plain from South Carolina to Alabama. Means et al. (1996) documented a decline in occurrence of that species in Florida associated with conversion of longleaf pine (*Pinus palustris*) savannah to slash pine (*P. elliottii*) plantations. Longleaf pine habitat in the Southeast has been largely converted to other uses during the past 200 years.

The North American paradox

The pattern of declines in North America is mysterious. Habitat alteration is still thought to be the primary cause of declines, but relatively few declines have been described in the East, which has the majority of the human population and landscapes that have been extensively transformed by urbanization and agriculture. For example, Fahrig et al. (1995) found a negative relationship between intensity of vehicular traffic and anuran density in Ontario, and Delis et al. (1996) observed lower amphibian diversity in a low-density urban development in Florida than in nearby undeveloped areas. Amphibian species richness in eastern Canada is negatively correlated with agricultural intensity (Hecnar and McCloskey 1996; Bonin, DesGranges et al. 1997; Hecnar 1997). This contrasts to the West, with fewer humans and more of the landscape protected from alteration by national parks and wilderness areas. One hypothesis is that habitats for western amphibians are set in relatively arid landscapes with limited opportunities for dispersal among populations. Re-colonization and recovery are normally slow in that region and are further

reduced or precluded by habitat fragmentation (Blaustein, Wake et al. 1994); therefore, declines may have more often resulted in regional extinction.

However, there are reasons why this paradox of East versus West may be illusory. First, it is an oversimplification and exaggeration to state that western population declines have occurred in pristine habitats. Many declines of western amphibians have occurred in California, which has most of the West's human population and agricultural development. For example, Fisher and Shaffer (1996) found severe declines in amphibian populations in the Sacramento and San Joaquin valleys, and Jennings (1995) described declines of ranid frogs as being most severe in agricultural and urban areas. Although Drost and Fellers (1996) described declines of population sizes in several species in relatively undisturbed or protected habitats in the Sierra Nevada, these areas are subject to atmospheric deposition of pesticides and other contaminants from the heavily agricultural Central Valley of California. There are actually few or no "pristine" habitats in western North America. For example, Bahls (1992) estimated that 95% of high-elevation lakes in the western U.S. were originally fishless, but in order to enhance recreational fisheries, most now have been stocked with trout, mainly species not native to the West.

Second, it is possible that some declines in the East have gone unrecognized. Fewer surveys have been completed in the East, probably because most amphibian habitat occurs on private lands and access is more difficult than on the extensive public lands in the West. Also, just as amphibian population declines may be more obvious in the West because habitats are relatively isolated, declines in the East may be much less obvious because habitat is plentiful and some amphibians usually can be observed. But presence of a species does not necessarily imply that a healthy population occurs at that location. Amphibian populations frequently exist within a source-sink metapopulation structure (Gill 1978; Sjögren 1991; Sjögren Gulve 1994; Seburn et al. 1997). Explosive reproduction produces extremely variable population sizes (Pechmann et al. 1991; Pechmann and Wilbur 1994; Green 1997b), and, in successful years, dispersing individuals from source populations may occupy marginal habitats or rescue populations already occurring in them (Sjögren Gulve 1994). One result may be that declines of source populations are more difficult to detect because they are embedded in a noisy background of constantly shifting occupancy of suitable and less-suitable habitats.

Declines in Central and South America

The golden toad (*Bufo periglensis*) is arguably the flagship species for the issue of amphibian population declines. This distinctive species occurred in a small area of the Monteverde cloud forest in Costa Rica. Declines in population size were first noticed in 1987, when 1500 adults were observed but only 29 tadpoles survived to metamorphosis (Crump et al. 1992). No toads have been observed since 1989

(Pounds and Crump 1994; Pounds et al. 1997), and the golden toad is probably extinct.

Several other species, including the harlequin frog (*Atelopus varius*), declined or disappeared from Monteverde at the same time (Pounds and Crump 1994; Pounds et al. 1997). In all, approximately 50% of the expected 50 species of anurans were absent in 1990, some of the surviving species were reduced in abundance, and few of the missing species have recolonized the area since (Pounds et al. 1997). Pounds and Crump (1994) noted that the 1987 population crash coincided with the strongest El Niño/Southern Oscillation on record to that date and suggested several possible causes for the decline. The unusually warm and dry conditions could have killed amphibians directly, altered animals' immune systems to increase susceptibility to disease, or concentrated atmospheric contaminants to lethal concentrations.

A second Costa Rican frog decline occurred at another cloud forest location 250 km southeast of Monteverde (Lips 1998). The anurans *Atelopus chiriquiensis*, *Rana vibicaria*, *Hyla calypsa*, *H. rivularis*, *Bufo fastidiosus*, *Eleutherodactylus punctatolius*, and *E. melanostictus* and the salamander *Oedipina grandis* were absent or reduced in number on transects sampled from 1993 to 1996 compared with numbers from 1991 and 1992. Lips (1997) also found 54 dead or moribund individuals from 10 species along streams at a site in Panama. Lips (1998) suggested that either contaminants or disease was the most likely cause of the declines she observed.

In the Caribbean, several species of coquis (*Eleutherodactylus*) and the ridge-headed toad (*Pellodytes lemur*) have declined in Puerto Rico. Both the ridge-headed toad and golden coqui (*E. jasperi*, not seen since 1981) are listed as endangered, and the latter and two other species may be extinct (Joglar and Burrows 1996; Wiley and Vitella 1998). The web-footed coqui (*E. karlschmidti*) has not been observed since 1974, and the mottled coqui (*E. eneidae*) was last seen in 1990. Three coquis, the mottled, forest (*E. portoricensis*), and ground (*E. richmondi*), have disappeared from two high-elevation sites in the Luquillo Experimental Forest (Woolbright 1997). Habitat destruction by Hurricane Hugo in 1989 apparently contributed to the decrease in occurrence of the latter two species, but the mottled coqui was gone before the hurricane.

The diverse anuran fauna at Boracéia, a mountainous site (900 m elevation) on the Atlantic Coast of Brazil, has been observed periodically for 50 years. Several species disappeared or declined in 1979 (Heyer et al. 1988, 1990). Five species, common before 1979, are apparently extinct, and a treefrog (*Fritziana ohausi*) associated with bamboo (*Merostachys* spp.) has not been detected. Severe declines in abundance occurred in six other species. As of 1994, species that had disappeared completely in 1979 were still missing, but at least one species (*Schizocorymbus*) that had decreased in occurrence was once again abundant (Bertolucci and Heyer 1995). The decline at Boracéia was attributed to an unusually severe frost (4 days of temperatures below freezing) in 1979 (Heyer et al. 1988).

Also on the Atlantic Coast of Brazil, Weygoldt (1989) described the disappearance or population declines between 1981 and 1986 of eight species of stream-dwelling anurans, closely related to species at Boracéia. Weygoldt (1989) observed several dry winters at his site but also suggested that both the population declines he observed and the ones at Boracéia could have been caused by acid rain. Heyer et al. (1988, 1990) argued that pollution was unlikely to have caused the declines in populations at Boracéia.

La Marca and Reinhaller (1991) observed declines in occurrence of five species of bufonids (*Ateleopus*) in the Venezuelan Andes. They discussed several possible causes for these declines, but there was little evidence to support anything specific.

Another species, *A. ignescens*, appears to have declined in the high Andes of Ecuador (Stebbins and Cohen 1995).

Declines in Australia

A second "cover model" for declines in amphibian populations is the gastric brooding frog (*Rheobatrachus silius*) from the mountains of southeastern

Queensland, eastern Australia. This frog, discovered in 1973, and its congener, *R. villinus*, are unique in that the young develop in the stomach of the mother (Stebbins and Cohen 1995). Unfortunately, both species and another stream-dwelling species, the southern dayfrog (*Taudactylus diurnus*), appear to have gone extinct shortly after 1980 (Blaustein and Wake 1990; Stebbins and Cohen 1995; Laurance et al. 1996). Those losses were the first of a series observed in montane stream frogs in eastern Australia. Richards et al. (1993) and Trenerry et al. (1994) described population disappearances or declines in population sizes of six species from high-elevation sites surveyed in 1991 to 1993, although some of these species were still common at lower elevations. Laurance et al. (1996) list 14 species of frogs that have shown a decline in occurrence in the mountains of eastern Queensland and northeastern New South Wales, and Mahony (1996) lists 10 species that have disappeared and 16 species that have declined along the east coast of Australia. Laurance (1996) analyzed weather data, and although wet-season rainfall was reduced in the five years preceding declines, he concluded this was insufficient to have caused the declines. Laurance et al. (1996) hypothesize that epidemic disease was the most likely explanation, a conclusion strongly disputed by Alford and Richards (1997). The species that have declined in eastern Queensland share several ecological characteristics, including small clutch size, habitat specificity, and breeding in streams (Williams and Hero 1998). This is suggestive that a common factor is involved in these losses.

The corroboree frog (*Pseudophryne corroboree*), another montane endemic, has declined in occurrence in part of its range in the Snowy Mountains of New South Wales (Osborne 1989). A severe drought in 1982 may have been at least partly responsible for this decrease. Mahony (1993) failed to find 5 of the 30 species of hybrid and myobatrachid frogs that reputedly occurred in the Watagan Mountains of

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New South Wales. Two of these were stream species, but two breed in ephemeral water and one breeds in ponds.

The green and golden bell frog (*Litoria aurea*) is a pond breeder that is an exception to the trend of population declines in endemic, high-elevation stream species in the tropics. Those species and two closely related sibling species were widely distributed in southeastern Australia, but they have undergone extensive declines throughout most of their ranges (Osborne et al. 1996; White and Pyke 1996; but, see Gillespie 1996). Declines in populations of green and golden bell frogs were associated with droughts from 1979 to 1982 (Osborne et al. 1996). Introduced mosquitofish (*Gambusia holbrooki*) are also present in many former frog habitats; laboratory and field experiments demonstrated that mosquitofish prey on bell frog tadpoles (Morgan and Buttner 1996).

Declines in Europe, Asia, and Africa

Declines in amphibian populations have been observed on most continents in the past decade, but most surveys and research have taken place in North and South America and Australia. This implies not that declines have not taken place elsewhere, rather that documentation has usually been of a single species or in relatively small geographic regions. For example, natterjack toads (*Bufo calamita*) have declined in occurrence in Britain during the past several decades (Beebee 1976). Changes in habitat structure attributable to changing land use (Beebee 1977; Fleming et al. 1996) and anthropogenic acidification of breeding ponds (Beebee et al. 1990) appear to be the main causes of this decline. Numbers of populations of crested (*Triturus cristatus*), smooth (*T. vulgaris*), and palmate (*T. helveticus*) newts in southern England have declined in the past 20 years, because of habitat loss (Beebee 1997). Common toads (*B. bufo*), green toads (*B. viridis*), fire-bellied toads (*Bombina bombina*), and common frogs (*Rana temporaria*) have declined in southern Scandinavia (Andrén and Nilson 1981; Hagsström 1981; Semb-Johansson 1989). Acidification appears to have caused the decline of common frogs in Sweden (Hagsström 1981), and, likewise, Leuven et al. (1986) reported reduced amphibian diversity in acidified ponds in the Netherlands.

Other examples, however, may not qualify under Green's definition for decline in amphibian populations. Most of the Scandinavian examples of decreases in numbers of populations are of species within the northern limits of their ranges (Andrén and Nilson 1981) or are declines of abundance within populations (Semb-Johansson 1989). Kuzmin (1995) lists several species from the former Soviet Union in need of conservation, including the newts *Salamandra salamandra*, *Triturus alpestris*, *T. dabrygicus*, *T. karelinii*, *T. montandoni*, and *T. vittatus*; the toads *Bombina variegata*, *Pelodytes caucasicus*, *Bufo calamita*, and *B. verrucosissimus*; and the frogs *Rana dalmatina* and *R. macrozemis*. However, data on these possible population declines are incomplete, and information on trends from Asian Russia is particularly scanty (Kuzmin et al. 1995; Ravkin et al. 1995). Misayura et al. (1995) state that most species

in Ukraine have declined in occurrence, especially common toads and common frogs. Industrial and agricultural pollution were listed as the most important threats to amphibians in eastern Europe, and radiation from the Chernobyl disaster has caused increased mutation rates and chromosome abnormalities in common frogs and moor frogs (*R. arvalis*) in Belarus (Pikulik 1995).

Relatively little has been published to date on the status of amphibians in much of Africa and Asia. Logistic constraints and the existence of fewer trained local biologists than in North America and Europe are obvious hindrances to assessing population status of amphibians. Considerable work in basic faunal surveys is still being done (e.g., Raxworthy and Nussbaum 1996). These types of studies are valuable and generate baseline data necessary for evaluating future trends, but they provide little insight into recent population trends.

Causes of Declines in Amphibian Populations

The documented and hypothesized causes of declines in amphibian populations fall into three categories: habitat destruction and alteration, global anthropogenic influences, and natural causes. I will not review all of these in detail because some are the subjects of other chapters in this volume. I will discuss effects of introduced predators and increasing ultraviolet radiation more thoroughly because these factors represent extremes in our ability to explain and possibly reverse declines.

The first real controversy on the issue of whether declines in amphibian populations were occurring concerned the nature of population processes and whether unexplained declines could be explained by variation in population size. Pechmann and Wilbur (1994) argued that the number of unexplained declines might not be excessive, citing the high temporal variability in sizes of amphibian populations (Pechmann et al. 1991) and lack of evidence for factors other than habitat destruction. Blaustein (1994) countered that data on declines were available and that several long-term studies demonstrated population declines. Blaustein, Wake et al. (1994) analyzed long-term population data for 17 species and concluded that six showed trends of significant reductions in population size. Other authors (Corn 1994; Osborne et al. 1996) have also argued that rapid, range-wide declines in occurrence of widely distributed, abundant species were unlikely to be the result of natural fluctuations in population size. Pounds et al. (1997) evaluated the population declines at Monteverde, Costa Rica, and found the probability of losing 40% of species to chance within five years to be extremely small. They concluded that population losses were due to something other than random variation. Still, the dynamic nature of amphibian populations (Green 1997b, 1997c) suggests that the hypothesis that natural variation causes decreases will often be difficult to reject, particularly when single species are concerned.

Climate change is another factor implicated in numerous amphibian population declines. All amphibians depend upon water, either for breeding or water balance. Therefore, drought is obviously a serious challenge to population persistence (Corn and Fogleman 1984; Weygoldt 1989; Kagarise Sherman and Morton 1993; Pounds and Crump 1994; Stewart 1995; Osborne et al. 1996). Other extreme events, such as floods, frosts, and hurricanes, have been implicated as causes of declines at regional scales (Treyer et al. 1988; Corn 1994; Woolbright 1997).

Direct habitat destruction usually is cited as the most significant anthropogenic cause of loss of amphibian populations (Blaustein 1994; Pechmann and Wilbur 1994). Amphibian populations are often absent or degraded in urban and intensive agricultural landscapes (Ferraro and Burgin 1993; Delis et al. 1996; Fisher and Shaffer 1996; Bonin, DesGranges et al. 1997). Petranka et al. (1993) estimated that timber harvest in the Appalachian Mountains resulted in the annual loss of 14 million salamanders, and Corn (1994) suggested that because of long-term effects on habitat (Corn and Bury 1989), timber harvest in the Pacific Northwest had reduced regional abundance of stream-dwelling amphibians. But Ash and Bruce (1994) contended that the conclusions of Petranka et al. (1993) were overblown, arguing that effects of timber harvest are complex and vary geographically and among species, a view supported by the analysis of deMaynadier and Hunter (1995).

Habitat destruction and fragmentation may be the main reason for the declines in occurrence of many species, but indirect and more subtle effects on amphibians and their habitats probably pose the greatest threats to amphibians in the future. Global climate change is one of these indirect factors. Predicting the effects of climate change on amphibians is complicated by the interactions between the type of predicted change and the natural history of the species affected (Ovaska 1997). Drier climates are unlikely to be beneficial to amphibians, but warmer temperatures could be beneficial to species at high latitudes by increasing time available for growth and development. There is some evidence this is occurring. Some British amphibians are breeding significantly earlier now than they did 20 years ago (Beebe 1995), a result of the North Atlantic Oscillation (Forchhammer et al. 1998). However, the long-term effects on populations are unknown and are likely to be unpredictable, given the complex interactions of hydroperiod with predation and competition (Morin 1983; Skelly 1996). The association of declines in occurrence of tropical species with El Niño events (Pounds and Crump 1994) may be an example of effects of climate change.

The effects of contaminants on amphibians are covered elsewhere in this volume, but, despite considerable speculation (e.g., Stebbins and Cohen 1995), there is little evidence direct that contaminants have caused declines in occurrence of widely distributed species (e.g., Bradford, Gordon et al. 1994; Vertucci and Corn 1996). However, subtle effects of contaminants have been poorly studied. There are a variety of effects—particularly to growth, development, and behavior of larvae and juveniles—that could affect populations (Carey and Bryant 1995). The increased

prevalence of limb deformities found recently in the central U.S. (Helgen et al. 1998) has been suggested to be the result of contaminants. For example, Bonin, Ouellet et al. (1997) found a positive correlation between frequency of limb deformities in green frogs (*Rana clamians*) and agricultural intensity in Québec. However, limb deformities also may occur because of parasites (Sessions and Ruth 1990), and it is not yet evident whether limb deformities have resulted in declines in population sizes. Recently, Spauling and Fellers (personal communication) obtained evidence of reduced cholinesterase (ChE) activity in Pacific treefrog (*Hyla regilla*) tadpoles in the Sierra Nevada. The distribution and severity of ChE depression corresponded to areas in which native ranid species have declined or been extirpated, to the intensity of agriculture to the west of the Sierras in the Central Valley, and to reports of pesticides in snow and air. They suggested that pesticides may be implicated in the decline of ranids in the Sierra Nevada.

Carey (1993) hypothesized that contaminants could be the ultimate cause of disease in amphibians, acting to compromise the function of the immune system. Disease is the subject of considerable current discussion. Examples of diseases and infectious agents were reviewed by Crawshaw (1997). Blaustein, Hokit et al. (1994) and Kiesecker and Blaustein (1997) reported that the water mold *Saprolegnia* killed boreal toad and Cascades frog eggs in Oregon and that infection is exacerbated in large communal spawning sites. Cunningham et al. (1993, 1996) recovered poxvirus-like particles from dead common frogs after an episode of high mortality at several sites in England in 1992. Most recently, cutaneous infection by a chytrid fungus (Phylum Chytridiomycota) has been identified as the cause of death of rain-forest frogs in Australia and Central America (Berger et al. 1998). This is apparently the first reported parasitism of vertebrates by a member of this phylum. Similar cutaneous infection by the sacromycete *Basidiobolus* is apparently responsible for recent mortality of both wild and captive Wyoming toads (Taylor et al. 1995).

Laurance et al. (1996) postulated that a novel pathogen, possibly an iridovirus, is moving northward in eastern Australia at a speed of 100 km/yr, resulting in an "extinction wave." They suggested that the international trade in aquarium fish was a plausible source and vector for the pathogen. Lips (1998) extended this hypothesis to include all published declines of tropical amphibians in Australia, Costa Rica, and Brazil. The chytrid fungus identified by Berger et al. (1998) now seems to be a more likely agent than an iridovirus. However, Alford and Richards (1997) argued that much of the hypothesis of Laurance et al. (1996) was supported by speculation and insufficient data. Alford and Richards stated that the evidence for the "extinction wave" also could support a random pattern of extinctions or even an opposite, north-to-south pattern. In addition, Alford and Richards argued that the iridovirus claimed by some to be the pathogen has not been isolated from moribund frogs, while the chytrid fungus has; experiments demonstrating transmission of the pathogen were flawed; thermal environments of low- and high-elevation populations overlap, providing little protection for lowland frogs; and alternative explana-

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tions were dismissed without justification. Similarly, Aguirre (1994) criticized Carey's (1993) hypothesis as vague and her evidence of red-leg disease in Colorado boreal toads as insufficient to prove the presence of an infectious pathogen. Proof that disease has caused declines in population size or occurrence of amphibians is difficult to obtain and requires more data than currently are available (Crawshaw 1997).

Recently Cunningham et al. (1996) suggested that what has commonly been called red-leg disease is mainly caused by an iridovirus infection and not by *Aeromonas*. Similarly, mortality of Wyoming toads from fungal infection was originally thought to be red-leg disease. If red-leg has been misdiagnosed as a bacterial infection (bacteria are present, but are secondary invaders), the relatively common reports of mass mortality from red-leg (Crawshaw 1997) suggests that occurrence of iridovirus, and possibly fungi, in moribund individuals may not necessarily indicate attack by a novel pathogen.

Introduced predators in the mountains of western North America
Clearly, replacing a marsh with a subdivision or shopping mall results in the extinction of the frogs that resided in that marsh. Less obvious is that lakes in the Sierra Nevada, which look the same to us today as they did to John Muir a century ago, have been subjected to similar habitat destruction. Most high-elevation lakes in the western U.S. were historically fishless. Currently the majority have been stocked with non-native salmonid fish (*Oncorhynchus* spp., *Salmo* spp., *Salvelinus* spp.); (Bahls 1992; Knapp 1996). Trout have significant effects on some ranid frogs and ambystomatid salamanders but do not eliminate all amphibians from mountain lakes. In Rocky Mountain National Park in Colorado, the presence of *B. boreas* and boreal chorus frogs (*Pseudacris maculata*) were unrelated to presence of trout, but tiger salamanders were present at only one location that also had trout (Corn et al. 1997).

In 1978 and 1979, Bradford (1989) sampled 67 lakes in Sequoia and Kings Canyon National Parks in the Sierra Nevada and found that mountain yellow-legged frogs and fishes did not coexist in any of them, presumably because of predation by trout on tadpoles (Knapp 1996). Bradford et al. (1993) analyzed the distributions of fishes and mountain yellow-legged frogs in 95 basins (312 lakes) in these parks and found that the presence of fishes has fragmented remaining populations of frogs. Connectivity among populations of frogs has been reduced by an order of magnitude, and effective sizes are about one-fourth what they would be without trout present. In a 1989 re-survey of 45 of the 1978 and 1979 sites, the mountain yellow-legged frog was absent from 26 of 27 lakes where it had occurred before (Bradford, Graber et al. 1994). Two lakes that had lost frogs had gained fishes, but the cause of most disappearances was not obvious. However, increased fragmentation of frog popula-

tions probably was a factor because isolated populations have an increased risk of extinction from demographic processes (Sjögren 1991; Sjögren Gulve 1994).

Fish stocking was reduced in Sequoia and Kings Canyon National Parks in the 1970s and was eliminated in 1991 (Knapp 1996). Meanwhile, the California Department of Fish and Game continues to stock lakes in the national forest lands surrounding the parks. Very few of the national forest lakes are fishless, but non-native trout are disappearing from some lakes in the parks (Knapp 1996). Large populations of *R. muscosa* (100 to 500 adults) are now present at several sites from which fishes have disappeared (Knapp 1996).

Tyler, Liss, Cranio et al. (1998) found severe reductions of densities of long-toed salamander (*Ambystoma macrodactylum*) larvae in lakes containing trout in North Cascades National Park, Washington. They observed 913 larvae in 10 lakes without fishes, 98 larvae in 5 lakes with non-reproducing populations of fishes, and 18 larvae in 5 lakes with reproducing fish populations. However, the effect of fishes on salamanders was mediated by water chemistry. In lakes with high nitrogen concentrations (and greater abundance of crustaceans), salamander larvae were significantly more abundant in lakes without fishes than in lakes with fishes. In lakes with low nitrogen, however, there were no differences in larval abundance between lakes with or without fishes. Abundance of all vertebrates and invertebrates was low in lakes with low productivity (i.e., low nitrogen). In experiments in artificial ponds, survivorship and size of long-toed and Northwest salamander (*A. gracile*) larvae was lower in the ponds with trout (Tyler, Liss, Hoffman et al. 1998). Larvae of both species used a narrower range of habitats in the presence of trout.

A situation similar to western North America also occurs in the mountains of northern Spain, where salmonids also have been stocked in historically fishless waters. Braña et al. (1996) found that most lakes with fishes contained either zero or one species of amphibian, but lakes without fishes harbored three to five amphibian species.

Management of lacustrine habitats for recreational fisheries was long accepted as appropriate (Fraleley 1996), but this attitude may be changing, particularly in wilderness areas (Duff 1995). The negative effects on native lake biota, and many of the logistic requirements of fish stocking (e.g., use of aircraft) may not be compatible with wilderness values mandated under the Wilderness Act of 1964; however, the Act also states that it cannot be interpreted as interfering with state responsibilities for fishes and wildlife in national forests. These contradictions require cooperation between state and federal governments in managing wilderness lakes (Fraleley 1996). Non-native fishes can be removed from lakes using chemicals or nets (Knapp and Matthews 1998). Recovery of amphibian populations in lakes from which trout have been removed (Knapp 1996) and changing attitudes about how wilderness lakes should be managed (Duff 1995; Fraley 1996) suggest that plans to restore amphibian populations could succeed in some situations.

Ultraviolet B radiation

Biologically significant ultraviolet radiation occurs in the wavelengths 280 to 320 nm (ultraviolet B [UV-B]) and 320 to 400 nm (ultraviolet A [UVA]). UV-B is absorbed by nucleic acids, resulting in creation of cyclobutane pyrimidine dimers (CPDs), photoproducts that are mutagenic because they block transcription (Blaustein, Hoffman et al. 1994; Hays et al. 1996). Exposure to UVA may cause cellular and DNA damage (Hays et al. 1996), but UVA also may stimulate photoactivation, or repair of CPDs. The enzyme photolyase is key to photoactivation, and the concentration of photolyase in amphibian eggs varies considerably among species. Amphibian eggs that are exposed to sunlight (e.g., from species that oviposit in the shallow margins of ponds) have greater photolyase activity than do eggs that typically are not exposed to sunlight, such as eggs of terrestrial salamanders, which are deposited in subterranean nests (Blaustein, Hoffman et al. 1994; Hays et al. 1996).

The UV-B radiation that reaches the earth's surface is significantly reduced by stratospheric ozone, and there are steep latitudinal, elevational, and seasonal gradients in UV-B radiation because of changing solar angles and variation in ozone thickness (Caldwell et al. 1980, 1986; Caldwell and Flint 1994). UV-B is more intense closer to the equator, during the summer solstice, and at higher elevations. However, recent anthropogenic reduction of stratospheric ozone has caused an increase of 5 to 10% per decade since 1979 in UV-B radiation reaching parts of the earth's surface (Herman et al. 1996). This increase has occurred mostly above 40° latitude and is accentuated in early spring in the northern hemisphere (Kerr and McElroy 1993; Herman et al. 1996).

Increasing UV-B radiation is an inviting hypothesis to explain mysterious, sudden, relatively synchronous declines of species in pristine environments, such as the decline of boreal toads in the southern Rocky Mountains. Worrest and Kimmeldorf (1976) observed mortality and deformities of boreal toad embryos and tadpoles exposed to enhanced UV-B radiation in the laboratory. More recently, Blaustein, Hoffman et al. (1994) reported results of field experiments in Oregon that show mortality of amphibian embryos exposed to ambient UV-B in sunlight. Boreal toads and Cascades frogs had lower hatching success in field enclosures exposed to full sunlight compared with enclosures with UV-B filtered out. There was no difference among UV treatments in hatching success of Pacific tree frog (*Tytila regilla*) embryos. Activity of photolyase, extracted from the eggs of these species, was congruent with the results of the field experiments. Pacific tree frogs had significantly greater photolyase activity than did either Cascades frogs or boreal toads. Blaustein et al. (1995) observed similar results for Northwestern salamanders. Hatching success was severely reduced in full sunlight. Photolyase activity in Northwestern salamander eggs (Blaustein, Hoffman et al. 1994) was similar to that in boreal toad eggs but was about one-seventh the activity in Pacific tree frog eggs. Blaustein et al. (1997) exposed embryos of long-toed salamanders to ambient UV-B and again

observed severely diminished survival and high rates of malformation in comparison to embryos shielded from UV-B. Conversely, exposures of northern red-legged frog embryos to ambient sunlight and sunlight with UV-B removed showed no reduction of hatching success, and red-legged frog eggs had high photolase activity (Blaustein et al. 1996).

Anzalone et al. (1998) conducted a field experiment in southern California similar to the studies from Blaustein's lab in Oregon. Embryos of the California tree frog (*Hyla cadaverina*) and California newt (*Taricha torosa*) exposed to ambient UV-B had lower instances of survival than did embryos exposed to light from which UV-B was removed. Survival of Pacific tree frog embryos was unrelated to UV-B, agreeing with the results of Blaustein, Hoffman et al. (1994). Lizana and Pedraza (1998) also conducted field experiments in Spain similar to those in Oregon and found high mortality of common toad embryos, but not of natterjack toad embryos, exposed to ambient sunlight.

The apparent sensitivity of some amphibian species to current levels of UV-B radiation has led some authors to hypothesize that increasing UV-B has contributed to global declines in amphibian populations. However, the results of the Oregon studies have been criticized for a number of reasons, including in adequacy of experimental design and failure to exclude confounding variables (Licht and Grant 1997). One problem with the Oregon studies is indicated by results of an experiment by Kiesecker and Blaustein (1995), who found that there was no increase in mortality of boreal toad embryos exposed to ambient sunlight if the fungus *Saprolegnia* was removed from the water. No other field studies of UV-B and amphibians have controlled for the presence of *Saprolegnia*; therefore, conclusions that embryo mortality is attributable to UV-B are suspect.

In addition, several other studies apparently contradict the Oregon results. Grant and Licht (1995) and Ovaska et al. (1997) exposed embryos of several Canadian species to UV-B in the laboratory and did not observe increased mortality at current UV-B doses. Long et al. (1995) exposed northern leopard frog embryos to UV-B doses predicted to occur with current trends of ozone thinning and found an increase in mortality only when increased UV-B was combined with low pH. van de Mortel and Buttemer (1996) obtained ambiguous results in field experiments with green and golden bell frogs in Australia. One set of experiments showed increased mortality of embryos, but a second experiment failed to repeat these results. Corn (1998) conducted field experiments on boreal toad embryos in Colorado, and there was no relationship between UV-B radiation and mortality. A second experiment tested the hypothesis that the different results of studies in Oregon and Colorado were due to geographic variation in sensitivity of boreal toads to UV-B. Toads were obtained from four locations (Washington, Montana, Colorado, and Utah), and embryos were exposed to fractions of ambient UV-B in a common experimental design. However, no significant relationship between embryo mortality and UV-B dose was found (Corn et al. unpublished).

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Both Cascades frogs and boreal toads are abundant in the blast zone at Mount St. Helens, Washington (Crisafulli and Hawkins 1998), which is now mostly open to sunlight. This situation does not support the hypothesis that declines in amphibian population size or occurrence are caused by increased UV-B. Anzalone et al. (1998) hypothesized that removal of chaparral overstory by fire could expose amphibians in California to increased UV-B. However, this does not seem to be a problem at Mount St. Helens, where the overstory has been absent for 18 years.

Dosages of UV-B to which amphibians are exposed have been poorly studied, and this has been one of the most persistent criticisms of field studies of effects of UV-B on amphibians (Roush 1995; Licht and Grant 1997). Corn (unpublished) used satellite-based measurements of UV-B (Herman et al. 1996) and long-term observations of amphibian breeding phenology to evaluate the variability in UV-B exposure. UV-B varies annually because of weather conditions and seasonally because of solar angle. Amphibian breeding activity varies annually within populations by up to 30 days because of weather and up to two weeks between populations across short (100 to 500 m) elevation gradients. The interaction between variable UV-B and timing of breeding results in annual UV-B exposure that can vary by more than 75% both within populations and between nearby populations separated by elevation. This variation is considerably greater than the increase in UV-B attributable to thinning ozone and casts additional doubt on the hypothesis that increasing UV-B is a significant cause of amphibian declines.*

Conclusions: Is There a Global Cause for Unexplained Declines?

Relatively few amphibians that have declined in Europe and temperate North America lack a plausible explanation for their status. Most often the cause is anthropogenic. Habitat alteration and destruction are the primary causes of amphibian declines in developed countries. In the tropics, however, the search for global explanations continues. Two global causes have been proposed in the recent literature: disease and increased UV-B radiation. In my opinion, neither can be unequivocally supported.

In the absence of convincing data on the etiology and epidemiology of amphibian diseases (Alford and Richards 1997), it is difficult to separate the disease hypothesis (Laurance et al. 1996; Lips 1998) from habitat destruction or alteration. Further, we know little of the ecology of many tropical species and the amount of environmental

* Editor's note: One possibility that deserves further investigation, however, is the possibility that UV-B interacts with anthropogenic contaminants and alters their toxicity. In some studies (see Chapter 8a, this volume, for a more complete review) the addition of UV-B under laboratory conditions increased toxicity of benz[a]pyrene and others contaminants by 100-fold or more. These studies suffer some of the same problems mentioned above including inadequate documentation of the UV-B dose.

change necessary to endanger them. Most declines of tropical amphibian populations have occurred in specialized, endemic species. Those traits make these species more sensitive to environmental change (Leigh 1981; Rabinowitz et al. 1986). Even if disease is the main cause of death for tropical amphibians, it may not result from novel pathogens, but from stress induced by changes in the environment (Carey 1993).

The hypothesis that increasing UV-B radiation has caused amphibian population declines suffers from conflicting results of several studies and an inability to separate confounding variables from field experiments. Additionally, areas of the earth with large numbers of declining amphibians do not coincide with regions receiving increased UV-B. In areas that have seen increased radiation, natural variation in the UV-B dose to which amphibians are exposed is at least 5 to 10 times the amount of increase due to thinning ozone. UV-B radiation is unlikely to be the global cause of unexplained decreases in amphibian population sizes or occurrence.

Considerable progress has been made in the past few years in verifying that decreases in population sizes are real and in identifying causes of declines. Most declines are caused by habitat alteration, and some are permanent. We cannot restore the vanished springs of the Las Vegas Valley and bring back the extinct leopard frog *Rana fisheri*. But other species may have hope. For example, the effects of introduced fishes on amphibians in high-elevation lakes are severe but reversible. Restoring amphibian populations is partly a political problem, requiring cooperation between different management agencies and the public. For unexplained declines, discovery that a common pathogen has killed frogs in Australia and Central America (Berger et al. 1998) is an important development. If this represents a novel pathogen, research on its etiology and methods for preventing its spread will be critical. Conversely, if the pathogen is the proximate result of stress attacking the immune system, identifying and ameliorating the stressors are more important tasks for conserving amphibians. Differentiating between these hypotheses is a high priority. Also important in the near future is understanding and predicting how populations will respond to changing climates. Amphibian populations that have shrunk will be vulnerable to climate change, and future plans to conserve populations will require thorough knowledge of the relationships between life history of amphibians and the physical environment.

Acknowledgments—I thank Mike Adams, Bruce Bury, Gary Fellers, David Green, Roland Knapp, and Hart Welsh for reading the manuscript and offering many excellent suggestions for its improvement.

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