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Numerous factors, such as global environmental changes, habitat destruction, introduced species, diseases, and chemical pollution, appear to be contributing to amphibian population declines. Moreover, the life history characteristics and behavior of many amphibian species appear to be placing them in jeopardy. Such behaviors and ecological attributes were molded over evolutionary time under selection pressures that acted on amphibians in a variety of ways. Many biologists who study amphibian population declines, however, have failed to consider some of these evolutionary aspects. Better understanding of amphibian population declines requires that scientists and policymakers consider the ecological processes associated with the declines in light of evolutionary principles such as these: Evolution is limited by historical constraints; not all evolution is adaptive; adaptations are often compromises; evolution can only alter existing variations; and evolution takes time.

Keywords: amphibians, population declines, evolution, UVB radiation, amphibian pathogens

Large losses in biodiversity are being documented around the world in almost all classes of plants and animals (Lawton and May 1995). Although the exact number of species being lost is unknown, some researchers estimate that the rate of extinction is greater than any known in the last 100,000 years (Wilson 1992). This biodiversity crisis is exemplified by the population declines and extinctions of amphibian species around the world (Blaustein et al. 1994a, 1994b, Houlahan et al. 2000, Stuart et al. 2004). In at least some cases, amphibian losses appear to be more severe than losses in other taxa (Pounds et al. 1997, 1999, Stuart et al. 2004). Moreover, declines in amphibian populations are prominent because many of them are occurring in areas that remain relatively undisturbed by humans, such as national parks, conservation areas, and rural areas some distance from urban centers.

There is concern about amphibian population declines in part because many biologists consider amphibians excellent indicators of environmental change and contamination (Blaustein 1994, Blaustein and Wake 1995). Their skin is permeable and exposed (not covered by scales, hair, or feathers), and their eggs, which have no shells, may readily absorb substances from the environment. The complex life cycle of many amphibian species potentially exposes them to both aquatic and terrestrial environmental changes. These attributes, and the fact that amphibians are ectotherms, make them especially sensitive to changes in temperature and precipitation, and to other environmental changes such as greater ultraviolet (UV) radiation.

There appears to be no single cause for amphibian population declines. Like other animals, amphibians are assaulted by a barrage of environmental insults that often act in a complex way (Blaustein and Kiesecker 2002). The causes for declines may vary from region to region and even among different populations of the same species. Synergistic interactions between two or more agents may be involved. There may be interspecific differences, as well as differences between life stages, in how amphibians react to a potentially damaging agent.

Numerous factors, such as global environmental changes, habitat destruction, introduced species, diseases, and chemical pollution, appear to be contributing to amphibian population declines (Lannoo 2005). Adding to the complexity associated with amphibian population declines are observations that the behavior and life history characteristics of many amphibian species appear to place these animals in jeopardy. Such behaviors and ecological attributes were molded over evolutionary time under selection pressures that acted on amphibians in a variety of ways. Many biologists who study amphibian population declines, however, have failed to consider some of these evolutionary aspects. Better understanding of amphibian population declines requires that scientists and policymakers consider the ecological processes associated

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with the declines in light of evolutionary principles such as these: Evolution is limited by historical constraints; not all evolution is adaptive; adaptations are often compromises; evolution can only alter existing variations; and evolution takes time.

It is important to realize that much evolution occurs through genetic changes that affect rates of development and mechanisms that control specific biological processes. Furthermore, evolutionary changes occur at different rates and on different timescales, depending on the organism. For example, the evolutionary timescale may be in hours for bacteria, in weeks for certain fly species, and in decades for some vertebrate groups.

A historical perspective

Amphibians have evolved behaviors, morphologies, and lifestyles that have allowed them to persist for millions of years, since before dinosaurs existed on Earth and after dinosaurs' extinction. But under today's environmental conditions, these same behaviors and life history characteristics appear to be placing amphibians in harm's way. To illustrate these points, we explore amphibians' responses to two basic problems that many animals confront every day: (1) potential overexposure to sunlight with damaging UVB radiation and (2) exposure to diseases. These two problems are especially significant because they appear to be contributing factors in the declines of a number of amphibian populations around the world (Lannoo 2005).

The examples and generalizations described below may apply differently in different regions of the world, and may vary between species and even between life stages and populations of the same species. However, we believe our points about evolution are relevant to the phenomenon of amphibian population declines in general (figure 1), not only to the examples we provide.

Amphibian evolution and exposure to sunlight

Over evolutionary time, selection pressures have shaped the life history characteristics and behaviors of amphibians in ways that relate to their exposure to sunlight. Amphibians seek sunlight for thermoregulation and to maximize their growth and development. Especially in temperate regions, larvae often seek shallow, warm water, which ultimately results in an increase in their growth rate (Wollmuth et al. 1987). For example, Cascades frog (*Rana cascadae*) tadpoles are frequently observed in sunlit, warmer areas in the afternoon (Wollmuth et al. 1987). Mountain yellow-legged frog (*Rana muscosa*) tadpoles concentrate where water temperatures are highest (near the shore during the day, deeper in the late afternoon and evening; Bradford 1984). In one study, all but the latest-stage bullfrog (*Rana catesbeiana*) tadpoles selected the warmest microhabitats (Wollmuth and Crawshaw 1988).

Many frog species bask in sunlight for prolonged periods (Hutchinson and Dupré 1992). For example, Lillywhite (1970) found that more than 70 percent of the bullfrogs present in a pond were basking from 1:00 p.m. to 5:00 p.m. on a sunny day, compared with less than 20 percent on a cloudy day. An observational study of *R. muscosa* showed that each of eight frogs present in a pond had between 50 percent and 80 percent of its body exposed to full sunlight for half the sunlight hours (Bradford 1984). Juvenile western toads (*Bufo boreas*) often bask in the thousands along the shoreline (Blaustein et al. 2005a).

Many amphibian species lay their eggs in shallow, open water in direct sunlight (Behler and King 1979, Nussbaum et al. 1983, Ashton and Ashton 1988, Stebbins and Cohen 1995). Eggs that are in shallow water, or even floating on the surface of the water, develop in a more oxygenated environment and probably in areas with a lower risk of predator or parasite attacks. The oxygenation of eggs is critical to their development (Duellman and Trueb 1986).

In summary, amphibians living today often seek sunlight because, over evolutionary time, seeking sunlight has been beneficial for their thermoregulation, growth, and development, and perhaps for other reasons. Yet today's sunlight exposes amphibians to doses of UVB radiation that can kill or significantly damage them.

Ultraviolet radiation in ancient and modern sunlight

At the terrestrial surface, UVB radiation (with a wavelength of 320 to 290 nanometers [nm]) is extremely important biologically. Critical biomolecules absorb light with a higher wavelength (UVA, 400 to 320 nm) less efficiently, and stratospheric ozone absorbs most light that has a lower wavelength (UVC, 290 to 200 nm). UVB radiation can cause mutations and cell death. At the level of the individual, UVB radiation can slow growth rates, impair the immune system, and induce various types of sublethal damage (Tevini 1993). Numerous organisms, including algae, crop plants, fishes, humans, and many invertebrates, can be harmed by exposure to UVB radiation (van der Leun and Bornman 1998, Bancroft et al. 2007).

Animals have been exposed to sunlight and UVB radiation throughout their evolutionary history (Cockell 2001). Moreover, animals, including amphibians, have been subjected to periodic ozone depletion, with concomitant increases in UV radiation exposure. Natural events such as volcanic activity, supernova explosions, impacts from comets and asteroids, and solar flares can result in large-scale ozone depletion, with relatively rapid, transient increases in UV radiation (Cockell and Blaustein 2000, Cockell 2001). Ozone depletion may last for decades if an impact is large enough (Cockell and Blaustein 2000). On an evolutionary timescale, significant ozone depletion caused by impacts from comets and asteroids may be relatively common. Although ozone damage from such impacts is influenced by a variety of factors (Cockell 2001), one estimate is that significant ozone depletion from asteroid and comet impacts may occur at an average frequency of once every 800 years (Cockell 2001). Thus, over evolutionary time, UV radiation has been a ubiquitous stressor on living organisms (Cockell 2001).

To seek or not to seek sunlight

Exposure to "bursts" of UV radiation every few centuries most likely is not responsible for the situation facing organisms today. Human-induced production of CFCs (chlorofluorocarbons) and other chemicals continuously depletes stratospheric ozone, inducing long-term, persistent increases in UVB radiation at the Earth's surface (Solomon 1999, Cockell and Blaustein 2001). Furthermore, decreases in stratospheric ozone, along with climate warming and lake acidification, lead to lower concentrations of dissolved organic carbon (Schindler et al. 1996), which results in increasing levels of UV radiation in aquatic systems. Data from remote sensing indicate that levels of UVB radiation have recently risen significantly (especially since 1979) in both tropical and temperate regions (Kerr and McElroy 1993, Herman et al. 1996, Middleton et al. 2001), and amphibian populations are declining in these areas (Stuart et al. 2004). These data, in conjunction with mounting experimental evidence, suggest that increasing UV radiation is harmful to amphibians (Blaustein et al. 1998, 2001a).

Constraints

Examples regarding amphibians

Historical → Amphibians lay their eggs in water

Evolutionary compromises → Amphibians are exposed to numberous abiotic and biotic agents; adaptations are the result of numerous selection pressures

Not all evolution is adaptive → Basking and laying eggs in shallow water exposes amphibians to UVB; schooling increases likelihood of transmitting diseases

Evolution can only alter existing variations → Amphibians have thin, permeable skin; they do not have protective hair or feathers

Evolution takes time → Regardless of the intensities of selection pressures, adaptations may not evolve if not given enough time

→ Limited ability to adapt to extreme changes

Figure 1. Evolutionary constraints regarding amphibian population declines.

Exposure to UVB radiation may be especially significant for those amphibian species for which selection pressures have resulted in behaviors that expose them to relatively large doses of solar radiation. For example, as stated above, many amphibians lay eggs in open, shallow areas where they receive maximum exposure to sunlight. This exposure can heat egg masses, which induces faster hatching and development (Stebbins and Cohen 1995). Similarly, the larvae of many amphibian species seek shallow, open regions of lakes and ponds, where it is warmer and they can develop more quickly (Hokit and Blaustein 1997, Hoff et al. 1999). The rate of development is especially critical for amphibians living in ephemeral habitats. These species must metamorphose before their habitat dries or freezes (Blaustein et al. 2001b). Thus, amphibians are often faced with conflicting selection pressures. Some species must develop quickly, before their habitat disappears. Therefore, they seek sunlit areas, where exposure to warmer temperatures enhances development. Yet evidence from a number of recent studies illustrates that many amphibian species, even those that seek sunlight, are sensitive to damage from solar radiation (Fite et al. 1998, Belden et al. 2000). If exposed, amphibians may die or accrue potentially severe sublethal damage.

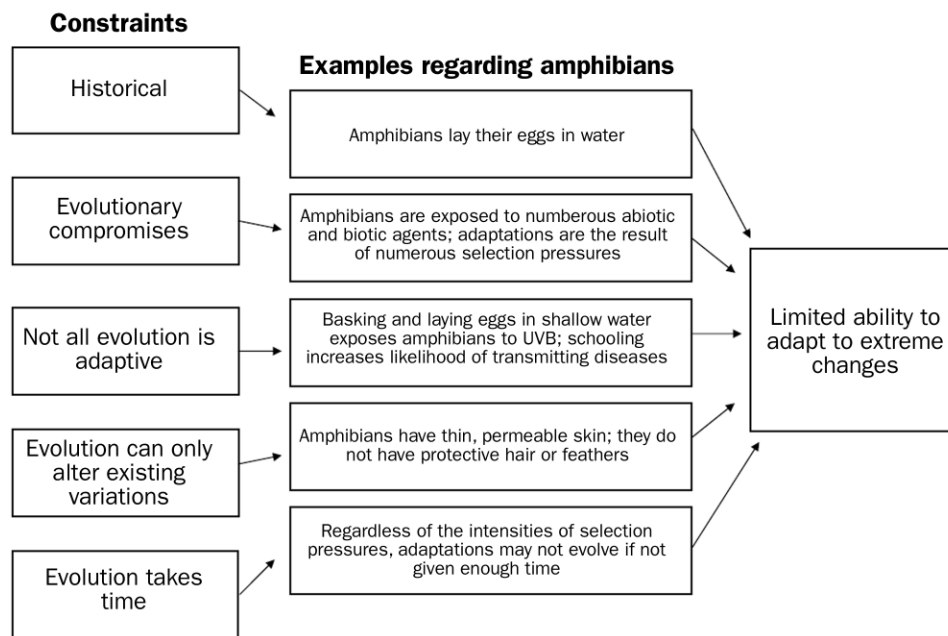UVB damage in amphibians has been well documented experimentally in the laboratory and in the field. In field experiments, investigators around the world have shown that ambient UVB radiation decreases the hatching success of many amphibian species in nature (Blaustein et al. 1998, 2001b). For example, in the Pacific Northwest of the United States, the hatching success of Cascades frogs, western toads, long-toed salamanders (*Ambystoma macrodactylum*), and northwestern salamanders (*Ambystoma gracile*) was lower when exposed to ambient UVB radiation than when eggs were experimentally shielded from UVB radiation (Blaustein et al. 1998). In California, the hatching success of California treefrogs (*Hyla cadaverina*) and California newts (*Taricha torosa*) was lower for eggs exposed to UVB radiation than for eggs that were experimentally shielded from UVB (Anzalone et al. 1998). In Europe, the hatching success of common toads (*Bufo bufo*) was lower for UVB-exposed eggs than for those shielded from UVB (Lizana and Pedraza 1998). The hatching success of moor frogs (*Rana arvalis*) increased when embryos were shielded from UVB (Häkkinen et al. 2001). In Australia, the hatching success of alpine treefrogs (*Litoria verreauxii alpina*) and eastern froglets (*Crinia signifera*) was significantly enhanced when embryos were shielded from UVB radiation (Broomhall et al. 1999).

For other amphibian species, hatching success is unaffected when eggs are exposed to ambient levels of UVB radiation in field experiments (Blaustein et al. 2001a). However, even though hatching rates of these species may appear unaffected by UVB in field experiments, a number of sublethal effects accrue after exposure. For example, exposure to UVB radiation may alter amphibians' behavior (Nagl and Hofer 1997, Blaustein et al. 2000, Kats et al. 2000), slow their growth and development (Belden et al. 2000, Smith et al. 2000, Pahkala et al. 2001, Belden and Blaustein 2002a), or cause cumulative

developmental and physiological damage (Worrest and Kimel-dorf 1976, Blaustein et al. 1997, Fite et al. 1998, Ankley et al. 2000). Developmental anomalies after exposure to UVB radiation can occur at all life stages, from extremely early embryonic stages (Scharf and Gerhart 1980, Elinson and Pasceri 1989) through adult forms living in nature (Fite et al. 1998, Blaustein et al. 2005a).

Several experimental studies illustrate that early exposure to UVB radiation causes delayed effects in later stages. For example, UVB radiation did not influence the hatching success of plains leopard frogs (*Rana blairi*), but larval growth and development was slower for frogs that were exposed to UVB as embryos (Smith et al. 2000). Embryos of the common frog (*Rana temporaria*) exposed to UVB showed no effects in terms of survival rates, frequency of developmental anomalies, or hatching size (Pahkala et al. 2001). However, larvae exposed to UVB radiation as embryos had more frequent developmental anomalies, metamorphosed later, and were smaller than larvae shielded from UVB as embryos (Pahkala et al. 2001). Ambient levels of UVB radiation had no effects on hatching success in red-legged frogs (*Rana aurora*) (Ovaska et al. 1997, Blaustein et al. 1998), but larvae exposed to UVB radiation as embryos were smaller and less developed than those shielded from UVB radiation (Belden and Blaustein 2002b).

Emerging diseases

In human and wildlife populations, diseases may become more prevalent when changes occur in the ecology of the host–pathogen relationship.

Amphibian malformations. Amphibian species that lay their eggs in water, and whose larvae must grow and develop in water, are subjected to a number of waterborne pathogens. One example is the parasitic flatworm *Ribeiroia ondatrae,* which is probably largely responsible for the increasing frequency of malformed amphibians in North America (Blaustein and Johnson 2003a, 2003b, Sessions 2003). Although malformed amphibians have been observed for about 300 years (Johnson and Chase 2004), reports of deformed amphibians with missing or extra limbs have increased dramatically. Contemporary observations appear to show more severe and frequent malformations than historical observations (Johnson and Chase 2004).

Eutrophication, a growing problem for ponds and lakes (Blaustein and Johnson 2003b), appears to be the catalyst driving the elevated parasitic infections that have been linked to amphibian malformations (Johnson and Chase 2004). With increasing eutrophication of freshwater ponds, due to fertilizer runoff and cattle grazing, shifts in the composition of the aquatic community occur (Johnson and Chase 2004). In many freshwater systems where eutrophication has taken place, small species of snails are replaced by larger species, such as those that are intermediate hosts of *Ribeiroia* (Johnson and Chase 2004). Apparently, eutrophication lowers the mortality rate of infected snails, thereby increasing the period

over which they release parasites. Such changes lead to an increase in amphibian infections and malformations (Johnson and Chase 2004). Because most amphibian larvae must remain in water for their entire larval period, they may be subjected to a growing number of parasite-infected snails in eutrophic systems.

Infectious diseases. Just as there have been benefits to seeking sunlight over evolutionary time, there have probably been numerous benefits over evolutionary time for animals to lay their eggs communally or to join groups (Hamilton 1971, Bertram 1978, Pulliam and Caraco 1984, Håkansson and Loman 2004). Individuals within groups may be able to find food more efficiently, avoid predators more successfully, or use resources more effectively (Hamilton 1971, Bertram 1978). Yet the egg-laying habits and social behavior of many extant amphibian species may be placing amphibians in danger of acquiring infectious diseases.

Two pathogens that affect amphibian populations are the oomycete *Saprolegnia* and the fungus *Batrachochytrium dendrobatidis* (Blaustein et al. 1994c, Rachowicz et al. 2005). Amphibians that lay their eggs in communal egg masses (Behler and King 1979, Nussbaum et al. 1983) are especially at risk of acquiring and spreading infectious diseases such as *Saprolegnia* at the egg stage (Blaustein et al. 1994c). In fact, for at least one species, it has been shown experimentally that egg masses laid later and closest to the communal mass are more likely to acquire *Saprolegnia* than eggs laid earlier and away from the communal mass (Kiesecker and Blaustein 1997a).

Larval behavior may enhance amphibians' susceptibility to diseases, and especially to *Batrachochytrium.* The larvae of several amphibian species can act as reservoirs for *Batrachochytrium* (Blaustein et al. 2005b), whereas the larvae of other species die from exposure to the fungus. Transmission of *Batrachochytrium* may be enhanced under several circumstances. For example, as ponds dry, concentrations of *Batrachochytrium* increase. This may be especially important in highly social tadpoles that form large schools, as do many species of toads (*Bufo* spp.). In large schools, which can comprise hundreds of thousands of individuals (Blaustein 1988), there is great potential for disease transmission. For many species, schooling may be the only social behavior, besides mating, in which individuals are in contact with conspecifics. Moreover, as larvae, many species are found in the same habitat with other anurans, and pathogens may be transmitted between species at the larval stage.

Even after metamorphosis, juvenile frogs and adults may congregate in large numbers. For example, in Oregon, western toads—often numbering in the thousands—metamorphose synchronously and remain in large aggregations (Arnold and Wassersug 1978, Samollow 1980, Blaustein et al. 2005a). Adults of many amphibian species congregate to breed in huge assemblages (Wells 1977). These large aggregations may enhance the probability of disease transmission.

Climate change, ultraviolet radiation, and disease: A complex relationship

Ecological systems are complex. Thus, like the causes of amphibian malformations, the influences on the prevalence and acquisition of infectious diseases are complex and often involve an interaction with environmental changes. For example, Kiesecker and colleagues (2001) found a significant relationship between the amount of precipitation during amphibian breeding and the water depth at which toad eggs developed. In dry years linked to El Niño events, western toad eggs developed in shallower water, and embryonic mortality was higher. Western toad eggs can be sensitive to ambient levels of UVB radiation, and dry conditions caused an increase in exposure of the eggs to UVB. The authors suggest that UVB could have contributed to higher rates of egg mortality in these years (Kiesecker et al. 2001). However, there is a complex relationship among climate change, UVB radiation, and outbreaks of disease. Kiesecker and colleagues (2001) showed that when water levels decrease, UVB exposure increases, and eggs become infected with *Saprolegnia* more readily than when water levels are higher. The increase in frequency and magnitude of El Niño events as a result of global climate change (Meehl and Washington 1996, Timmermann et al. 1999) could increase the exposure of amphibians to detrimental levels of UVB and raise the infection rates of *Saprolegnia* (Kiesecker et al. 2001).

Pounds and colleagues (2006) showed that changes in climate in the American tropics have probably led to more outbreaks of chytridiomycosis, the disease caused by *Batrachochytrium*. It appears that shifting temperatures in the region are the ultimate trigger for the expansion of *Batrachochytrium* into amphibian populations. Temperatures in many highland areas in the American tropics are shifting toward the optimum for *Batrachochytrium* growth.

The coupling of environmental changes and disease outbreaks in amphibians in North America and in the tropics is emblematic of the complexity and dynamics of the ecological processes influencing amphibian population declines worldwide (Blaustein and Dobson 2006). It is clear that organisms may not be able to adjust to such dynamics effectively before their populations are seriously depleted.

The limits of evolution

We have argued that the causes of amphibian population declines are complex, and that amphibians often behave in ways that may be detrimental to them under today's environmental conditions. In an evolutionary context (figure 1), the problems that amphibians face are unprecedented, and many amphibian populations are at risk. Numerous selection pressures act on amphibians, including various abiotic and biotic agents to which amphibians are exposed during their lifetime. Many of these agents of selection are intense and relatively new (e.g., increasing UVB radiation due to ozone depletion; chemical contamination). It is difficult to predict the direction a population will take in the face of both natural and rapidly mounting human-induced selection pressures.

Limited by historical constraints, many amphibians (especially frogs and toads) must lay their eggs in water. This exposes eggs not only to aquatic predators and competitors but also to a variety of abiotic regimes, both natural and human induced, that may be especially harmful to them under today's conditions. For example, the chemical contamination of aquatic systems that extant amphibians face has become far more extensive as a result of mining, industrialization, urban sprawl, and agricultural processes (Boone and Bridges 2003). Such contamination can be measured in hundreds of years—a rapid change, given that amphibians have been laying their eggs in less-contaminated water for millions of years.

Some of the constraints on amphibians may indeed be the reason why populations of these animals are declining more than populations of other vertebrate groups (Stuart et al. 2004; see discussions in Holt and Gomulkiewicz 2004, Bridle and Vines 2007). Although relatively rapid evolution may occur within some amphibian populations when a novel threat arises (Kiesecker and Blaustein 1997b), other threats—such as emerging infectious disease, perhaps coupled with environmental changes—may be too intense and too new for amphibians to cope with them. As stated above, the dynamics of amphibian population declines are complex, and as in all organisms, there is an interplay among many biotic and abiotic factors and environmental and genetic constraints (Holt and Gomulkiewicz 2004).

Not all evolution is adaptive. Many amphibians still lay their eggs in shallow water and in large communal masses, potentially subjecting the eggs to UVB radiation and infectious diseases. Many amphibians school in large numbers, many newly metamorphosed amphibians aggregate, and many amphibian species mate in large communal groups. These behaviors and ecological attributes have probably persisted, and were probably beneficial, for millions of years (Romer 1939, 1968). But under today's conditions, these very behaviors may subject amphibians to a variety of damaging agents, including UVB radiation and pathogens. So why do amphibians exhibit such seemingly maladaptive characteristics? Because evolution takes time, it is not perfect, and it can only alter existing variations.

Obviously, amphibians, like other organisms, have defenses against UVB radiation and diseases. Exposure to sunlight over evolutionary time has undoubtedly resulted in mechanisms that have helped animals to cope with UVB radiation (Epel et al. 1999, Hofer 2000, Cockell 2001). Animals can either prevent UV damage from occurring or repair damage once it occurs (Epel et al. 1999). Thus, amphibians may use molecular, physiological, and behavioral mechanisms to limit their exposure to UVB radiation, or they may somehow repair UVB-induced damage (Blaustein and Belden 2003). Similarly, all organisms have defenses against diseases. For amphibians, these include the immune

system and numerous peptides on the skin (Rollins-Smith and Cohen 2003, Rollins-Smith and Conlon 2005).

However, many selection pressures, especially those that are human induced, may be too intense and may have arisen too rapidly for amphibians to evolve adaptations to overcome them. For example, ozone depletion is a phenomenon initiated only decades ago by human impacts on stratospheric chemistry (Madronich et al. 1998, Solomon 1999, Hoppel et al. 2005). Thus, living organisms have been bombarded with constantly rising levels of harmful UVB radiation only for the past several decades. Increasing UVB radiation is therefore a relatively new selection pressure. For some species, populations may be adversely affected before behaviors limiting amphibian exposure to sunlight, and other defenses (e.g., DNA repair mechanisms; Blaustein et al. 1994a), can overcome strong established selection pressures for seeking warmth. It is likely that some species will continue to seek sunlight, and those species without effective defense mechanisms against the damage from UVB radiation will be harmed or die when exposed to UVB (Blaustein and Belden 2003). Moreover, numerous experimental studies have shown that some amphibians cannot repair UV-induced DNA damage effectively (Blaustein et al. 1994a), either because the synergistic effects of UVB with other factors render the repair mechanisms ineffective or, more likely, because the repair mechanisms are not efficient in light of current levels of UVB radiation.

Similarly, immune systems are not perfect—otherwise, organisms would not get sick. Since 1976, at least 30 new diseases have emerged, many triggered by recent changes in the Earth's climate (Epstein 1997). Climate changes have influenced the emergence of two amphibian pathogens, *Batrachochytrium* and *Saprolegnia,* as discussed above.

Finally, *evolution is a compromise.* Evolution does not result in perfect organisms. Because of the numerous selection pressures facing organisms and the lack of existing variation, it is not possible for evolution to mold the "perfect amphibian." Indeed, the notion of amphibians' evolving adaptations to cope with recent and intense selection pressures has been given some weight. For example, it has been stated that amphibians have a "high resistance" to UVB (Licht 2003), and it has been suggested that many amphibian "eggs are apparently well protected against even today's UVB levels" (Beardsley 2003). Yet this depends on the species, the species' life history stage, and the ecological context. For example, the eggs of some species do not have adequate defenses against UVB radiation, and they may be laid where they are subjected to lethal levels of UVB radiation (Blaustein et al. 1994a). We do expect and observe variation in how amphibians cope with UVB radiation, diseases, and other agents—not all members of a population are equally susceptible to the same stressor—but we do not expect to see amphibians evolve into perfect organisms in the face of potentially damaging factors.

Genetic variation, in conjunction with various selection pressures, leads to differential survival of individuals within a population. Certain combinations of traits may allow an organism to survive better when facing some selection pres-sures, but these traits may make the same organism more susceptible to other selection pressures. Because of this interplay between traits, adaptation can be limited under certain circumstances even when overall genetic diversity is high (Bridle and Vines 2007). If a population faces many pressures and fails to adapt to just one pressure, the population may not persist, resulting in local declines. Given adequate genetic diversity and potential for rapid adaptation, those individuals with characteristics that allow them to cope with mounting environmental changes, emerging diseases, and other stressors will produce more offspring than individuals without those characteristics. Perhaps for some of the amphibian populations containing such individuals, those attributes will be good enough to permit the species to persist for millions more years.

Acknowledgments

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