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Physical Stressors

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Introduction

Evaluating the role of physical stressors on amphibian population declines brings into focus significant shortcomings in data and theory that are essential for effective management of amphibian populations. While there is broad consensus in the herpetological community that many amphibian populations are threatened by decline or outright extinction (for a review, see Alford and Richards 1999), data and theory that are critical to take nontrivial management actions are lacking. Two persistent controversies illustrate the predicament. First, demonstration that specific population declines and extinctions are part of a global phenomenon is still elusive because of the variability of amphibian population sizes and the paucity of long-term demographic data (Pechmann et al. 1991; Pechmann and Wilbur 1994; Green 1997). Even large compilations of data (hundreds of individual studies) subjected to rigorous statistical analyses do not provide clear answers (e.g., see the recent exchange between Houlahan et al. 2000, 2001; Alford et al. 2001). There simply is no substitute for long-term demographic studies from sites around the globe.

The second controversy relates to the roles of specific stressors as sources of amphibian declines. While there is consensus about candidate stressors presumed to be responsible for population declines (e.g., habitat destruction, disease, climate change, contaminants, and ultraviolet-B [UV-B] radiation), and also broad agreement that declines are likely the result of the interaction of multiple stressors, there are essentially no data demonstrating causal relationships between particular stressors and their effects on populations. For example, the effect of increased UV-B radiation exposure on amphibian mortality rates in laboratory experiments, semi-natural field enclosures, and natural populations has been studied extensively (Blaustein, Hoffman, et al. 1994; Kiesecker and Blaustein 1995; Kiesecker, Blaustein, and Belden 2001). However, even if effects on mortality rates are accurate and unbiased (but see Licht and Grant 1997 for discussion), effects on individuals cannot be extrapolated to population-level consequences because demographic rates (mortality and fecundity) of populations are unknown.

Encroachment of human populations upon natural communities directly or indirectly causes many changes in the physical environment of native plants and animals. Stressors that are byproducts of human population growth and economic development often co-oc-

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cur with natural stressors, so it is likely that many animals already experiencing natural stresses of disease, competition, and predation may encounter a barrage of anthropogenic stresses. Physical stressors that may influence amphibian population declines have often been attributed to global changes and include 1) habitat alteration or destruction, 2) climate change, and 3) increased ultraviolet (UV) radiation (Phillips 1990; Blaustein 1994; Blaustein, Wake, and Sousa 1994; Corn 1994, 2000; Donnelly and Crump 1998; Carey et al. 1999; Semlitsch 2000). These global changes will manifest themselves in local areas by altering critical terrestrial and aquatic environments through changes in vegetation, soil moisture and compaction, temperature, and incidence of rare climatic events (e.g., flooding and droughts; Donnelly and Crump 1998). Our objectives in this chapter are to 1) review current information on physical stressors on amphibian population declines, 2) address the roles that changes in the physical environment could play in amphibian declines, 3) make predictions about the effects of physical stressors, and 4) determine what information is needed to evaluate the effects of physical stressors on amphibian populations.

Habitat Alteration and Destruction

Habitat conversion is the prime threat to the world's biodiversity and a significant part of the global change phenomenon (Vitousek et al. 1997). The best-documented cause of amphibian population declines is associated with habitat alteration (Alford and Richards 1999). For instance, logging exposes terrestrial amphibians to drastically altered microclimate regimes (Ash 1997). While the specifics of habitat alteration on amphibians are considered in Chapter 7, habitat alterations and destruction affect the local thermal and hydric properties of the environment for amphibians. Amphibians with complex life cycles have at least two critical habitats whose integrity is essential for population persistence: 1) aquatic habitat for breeding and larval development and 2) terrestrial habitat, often around wetlands, for feeding and overwinter hibernation (Semlitsch 1998).

The most obvious habitat changes may be direct changes in vegetation. These may be caused by clear-cutting (Dupuis et al. 1995; Ash 1997), suppression of fire and other agroforestry practices (Waldick et al. 1999), or vegetative succession in terrestrial environments. Although federal laws protect the terrestrial habitat around permanent wetlands to some extent, ephemeral wetland habitats are not similarly protected, even though they often harbor greater species diversity (Semlitsch and Bodie 1998). Therefore, changes in the terrestrial environment alone may reduce the quality of wetlands by increasing sedimentation from erosion, increasing local temperatures, and reducing pond hydroperiod. Wetlands separated from critical terrestrial habitat may, in turn, become essentially worthless to many amphibians, except colonist species (e.g., *Pseudacris* spp.) or habitat generalists (e.g., *Rana clamitans*).

Changes in the vegetative structure can alter local temperature, relative humidity, and soil moisture (Vitousek 1994; Murcia 1995; Alford and Richards 1999). All of these factors may test the physiological limits of some species or reduce their competitiveness in new environments. Alterations of habitat can also increase the amount of habitat edge. Edges may have decreased moisture availability and increased extreme temperatures, solar ra-

diation, and wind disturbance compared to forest interiors (Chen et al. 1995; Kapos et al. 1997; Turton and Freiburger 1997). While some species increase in relative abundance along habitat edges, others are adversely affected (Schlaepfer and Gavin 2001). For example, if insect abundance increases along forest edges (Didham 1997), amphibians that prey on insects may migrate to forest edges if they can tolerate the warmer and drier conditions there. Animals living along edges may have reduced rates of parasitism or predation relative to forest interiors. Because many amphibians spend all or a majority of their life in terrestrial habitats, the outcome of these changes may be the elimination of some species, alterations in abundance, or reduced individual quality (e.g., body size or reproductive condition).

Aquatic habitat is critical for most amphibian species to carry out larval development, for breeding, and/or to maintain body moisture. Amphibians inhabit a broad range of wetland types from ephemeral puddles, ponds, and streams to permanent ponds, lakes, and streams (Duellman and Trueb 1994). The extremes (puddles and permanent water bodies) serve as critical habitat for species with special adaptations and are, therefore, important habitats. The greatest species diversity, however, is found in ponds with intermediate hydroperiods (Heyer et al. 1975; Pechmann et al. 1989; Wellborn et al. 1996). These small ephemeral wetlands are often destroyed by draining or altered by impounding to make them more permanent, resulting in reduced species diversity or population extinction (Semlitsch 1998). Draining wetlands can remove breeding sites and fragment populations, thus increasing the probability of extinction (Alford and Richards 1999).

Climate Change

Climate is a major factor controlling biological diversity (McNulty and Aber 2001) and affects individuals, populations, species, communities, and ecosystems (Andrewartha and Birch 1954). Amphibians have been extant for more than 350 million years (Goin et al. 1978; Pough et al. 2001; Zug et al. 2001) and have experienced climatic change throughout their long evolutionary history. However, climate change could strongly affect ectothermic organisms and can be a form of physical stress if the rate of change exceeds the organisms' abilities to respond (IPCC 1996, 2001; Ovaska 1997; Carey et al. 2001). Although many believe that the causes of global environmental changes are uncertain, data on increasing atmospheric carbon dioxide and its relationship to increasing global temperatures are unequivocal (Vitousek 1994; Ovaska 1997; Hughes 2000; McNulty and Aber 2001).

Predictions and effects of climate change

The earth's climate has warmed during the last century (IPCC 1996, 2001; Jones et al. 1999), and most global circulation models predict that the earth's temperatures will continue to increase (IPCC 1996; McCarty 2001; McNulty and Aber 2001). Predictions of global climate change models include increased worldwide surface temperatures of 1.5 °C to 4.5 °C in the next 90 years, increased evaporation rates, increased global mean precipitation, summer continental drying and warming, a rise in global mean sea level, and an increase in rare climatic events (e.g., droughts, flooding, hurricanes, tornados; reviewed

by Gates 1993). Global climate change involves the simultaneous and rapid alteration of several key environmental factors (Aber et al. 2001); however, conducting multifactorial experiments at multiple sites to establish the link between climate change and changes in amphibian populations is difficult. Links between climate change and species or communities have been reported for several types of organisms including amphibians (reviewed in Hansen and Rotella 1999; Hansen et al. 2001; McCarty 2001). If global warming is a stressor for amphibians, experimental and observational studies of the effects of climate on amphibians can inform management decisions.

Climate change can act as a stress on amphibians (McCarty 2001). Amphibians occupy a diversity of habitats and display a diversity of life history strategies (Duellman and Trueb 1994). Therefore, amphibians might be expected to differ in their sensitivity and vulnerability to global change (Ovaska 1997). Early life history stages are probably more sensitive than post-metamorphic stages to change because early stages are typically confined to water (Ovaska 1997). Population sizes of amphibians appear to be sensitive to fluctuations in the amount and seasonality of precipitation, and these factors are likely to be at least as important as temperature in determining the distribution and abundance of organisms (McCarty 2001).

Effects of climate change

Climate acts locally, and its effects will be most apparent at the level of populations and metapopulations (McCarty 2001). Few studies, however, have linked climate change as the causal agent for changes in species at these levels (Hughes 2000; McCarty 2001). Temperature and water availability have direct and indirect effects on amphibians. While most studies have focused on the direct effects of these factors on organisms, several scientists have suggested that the indirect effects of climate on species are worthy of study (e.g., McKone et al. 1998; Visser et al. 1998; Buse et al. 1999). The interaction between temperature and precipitation makes it difficult to consider these climatic variables independently in analyses of amphibian decline data. Dry conditions (i.e., low relative humidity, low soil moisture) coupled with high temperature in a warming environment generate dehydrating conditions for most amphibians, and Waldman and Tocher (1998) suggest that desiccation is an incessant threat for these organisms. Long-term studies have demonstrated that rainfall variation affects hydroperiod variation, which affects amphibian abundance (Berven 1990; Semlitsch et al. 1996). Short-term variation in weather can affect amphibian populations (Waldman and Tocher 1998), but linking long-term changes in temperature and precipitation to changes in population size and structure is difficult (Carey et al. 2001; McCarty 2001).

Climate warming was not associated with declines of California red-legged frogs (*Rana aurora draytonii*) based on spatial analysis (Davidson et al. 2001) or with declines of 14 species of Australian rainforest frogs (Laurance 1996). While Laurance (1996) found reduced precipitation and higher temperatures during the years prior to Australian declines, he concluded that the rainfall and temperature patterns were not unique to the long-term record and that unusual weather was unlikely to have been the cause of frog extinctions.

Alford and Richards (1999) and Pounds (2001) have suggested that daily rainfall records are probably more informative than the monthly values used by Laurance (1996), but insofar as we know, this reanalysis has not been conducted.

Precipitation and temperature changes

Changes in temperature and precipitation would be expected to have a dramatic effect on amphibians. Temperature and precipitation are cues that initiate breeding activities in many amphibians (Duellman and Trueb 1994), and changes in these factors are known to affect breeding phenology. For instance, increased global temperatures have been linked to changes in the timing of reproductive activities (Terhivuo 1988; Beebee 1995; Ovaska 1997; Gibbs and Breisch 2001; Hansen et al. 2001), but it is not clear that shifts in phenology can be linked to changes in demographic processes. For example, early arrivals at breeding sites might be advantageous to amphibians because increased larval periods might result in increased body size at metamorphosis. Unfortunately, if adult amphibians arrived much earlier at breeding sites than their prey (e.g., insects), then the mismatched phenology of amphibians and their insect prey could result in decreased amphibian populations. For example, larval survival could decrease from indirect effects associated with food availability for adults immediately prior to their initiating breeding activities. Although hypothetical for amphibians, such mismatched phenologies of breeding adults and their prey have been observed in other vertebrates (Visser et al. 1998) and warrant attention in field studies.

Understanding potential consequences of changes in environmental temperature is complicated by the general ability of ectotherms to mediate temperature variation through physiological and behavioral mechanisms. Short-term physiological (acclimation), behavioral, and long-term evolutionary responses may allow some populations to withstand environmental changes that do not extend beyond their lethal tolerance limits. There is extensive inter- and intraspecific variability in sensitivity to temperature variation, demonstrating that thermal physiology can and does evolve along environmental gradients (see Angilletta et al. 2002). The nature and extent of evolutionary responses are hard to predict because they are determined by levels of genetic variation, strength of selection, and the thermal sensitivity of particular physiological functions (Angilletta et al. 2002).

Global warming is expected to shift species' ranges poleward and upward to higher elevations (Peters 1991). These large-scale patterns of change are consistent with a hypothesis that organisms are responding to recent climatic change (IPCC 2001). Increased temperatures have been associated with a poleward shift in distribution of several animal taxa (Payette 1987; Hersteinsson and MacDonald 1992; Dennis 1993; Parmesan 1996; Brown et al. 1999; Hill et al. 1999; Parmesan et al. 1999; Thomas and Lennon 1999). Elevational shifts in distribution of plants and animals in response to warming have also been reported for montane tropical species (Pounds et al. 1999; Still et al. 1999). The rate at which species' boundaries can change is key to understanding how species will respond to climate change (McCarty 2001). Amphibians will either move to new environments, adapt to warmer conditions, or die (Miles 1994). If the rate of temperature increase is greater than the ability of organisms to adapt, local extinctions may occur in the face of a warming climate (IPCC 1996, 2001). Warming causes changes in soil moisture, hydrology, and

plant associations that can alter habitat suitability and lead to increased habitat fragmentation (Ovaska 1997). Fragmented populations might be at a higher risk for extinction in altered habitats if the alteration renders the habitat less suitable for amphibians or if the surrounding landscape is too hostile, resulting in reduced movement among habitat patches.

In actuality, climate warming may result in both beneficial and adverse effects for amphibians (Ovaska 1997). Activity periods for some species may be constrained with increased temperatures (Ovaska 1997), while increases in temperature may be beneficial for temperate species in the winter. However, high temperatures coupled with decreased precipitation and increased evaporation could be deleterious (Ovaska 1997). Warming may be beneficial to temperate amphibians that breed in winter because they will have an extended period for development (Ovaska 1997). Additionally, because of the positive correlation between species richness and temperature, Hansen et al. (2001) predict increases in amphibian abundances with global warming. In contrast, decreased temperatures, predicted by more frequent occurrence of environmental extremes, may have negative effects on amphibians. Heyer et al. (1988) associated the faunal collapse at Boraceia, Brazil, with an unusual hard freeze, whereas Weygoldt (1989) proposed that dry winters during the 1980s were responsible for this crash. Conversely, Ingram (1990) attributed the loss of two frog species in southeastern Queensland to excessive rainfall in cooler months. MacCracken et al. (2001) predict snow cover in the mountains of western North America to be reduced in extent and duration, adversely affecting the region's montane amphibian populations. For example, because breeding phenology of montane amphibians is closely tied to the timing of snowmelt (Corn and Muths 2002), earlier breeding is likely. This phenomenon may already be occurring in some populations of boreal toads in Oregon (Corn 2003). One detrimental effect of earlier breeding could be increased exposure and mortality from late freeze events (Inouye et al. 2001).

El Niño Southern Oscillations

Measurements and coral cores indicate that El Niño Southern Oscillations (ENSO) events have been semi-regular features of global climate for at least the past several thousand years (Alexander and Eischeid 2001). The effects of ENSO events are only beginning to be examined, but they have been associated with reproductive failure in seabirds (Wingfield et al. 1999), reduced body size in iguanas (Wikelski and Thom 2000), and shifts in island food webs (Stapp et al. 1999). Amphibian declines have not been linked with the stronger ENSO events (Alexander and Eischeid 2001), but these events may affect amphibians. El Niño results in extreme temperature and precipitation events in different regions, and all countries from northern Mexico to the tip of South America, and northeastern Australia, experience anomalous conditions during ENSO events (IPCC 2001). In 1987, for example, northwestern Peru and southern Brazil was unusually wet, whereas northern Amazonia, the Altiplano, and northeast Brazil were dry (IPCC 2001). In Mexico, Central America, and the Caribbean, there were more winter precipitation and less summer precipitation (IPCC 2001).

Pounds et al. (1997, 1999) linked the 1987 faunal crash in Monteverde, Costa Rica, to drought associated with the 1987 ENSO event. A recent reanalysis of the Monteverde amphibian faunal dynamics by Pounds et al. (1999) also included other vertebrates. Anoline

lizard and bird populations have also changed during the same time interval that amphibians declined, suggesting that climate change was responsible for changes in all taxa. Pounds et al. (1999) showed that dry-season mist frequency decreased since the 1970s and atmospheric warming has raised the altitude of the cloud bank. While rainfall totals show no downward trend for the Monteverde region, the number of consecutive dry days in the dry season increased during ENSO warming events. Anuran declines were associated with mist-frequency patterns, and the abundance of four aquatic-breeding species decreased synchronously in 1987, 1994, and 1998 (although data for 1987 are not presented in Pounds et al. 1999) with the declines in 1994 and 1998 corresponding to increases in total number of dry days. Recently, droughts associated with an ENSO event reduced water depth in breeding ponds; this phenomenon was associated with increased UV-B exposure that led to lethal fungal infection in the northwestern United States (Kiesecker, Blaustein, and Belden 2001; Pounds 2001). Although Pounds (2001) claimed that large-scale climate change caused wholesale mortality in an amphibian population, evidence demonstrating a total crash was not presented. Long-term data are needed to describe the nature of population dynamics and to distinguish the effects of long-term climate warming and periodic events like ENSOs on amphibians (McGowan et al. 1998; Mullin 1998).

Stochastic weather events: Drought and hurricanes

Stochastic weather events like droughts and hurricanes can affect amphibian physiology and habitat structure, and may become more frequent with climate change (IPCC 2001). The decreased water availability and extreme temperatures characteristic of drought can either be unpredictable (e.g., temperate areas) or predictable (e.g., deserts). Regardless of uncertainty in its prediction, when drought occurs, it is likely to have strong effects on amphibians because of their limited capacity to control rates of evaporative water loss in desiccating environments. Drought may also result in increased exposure to contaminants or susceptibility to parasites (Pounds and Crump 1994).

Amphibian population decreases have been associated with drought (Corn and Fogelman 1984; Osborne 1989; Weygoldt 1989; Woolbright 1991; Fellers and Drost 1993; Stewart 1995). In 1983, dry conditions in Monteverde increased the vulnerability of harlequin frogs (*Atelopus varius*) to lethal parasites along a stream and inspired a climate-linked epidemic hypothesis (Pounds and Crump 1994). The faunal crash in the Monteverde cloud forest may relate to drought conditions and has been the subject of several studies (Crump et al. 1992; Pounds and Crump 1994; Pounds et al. 1997, 1999). While various hypotheses were advanced by Pounds and Crump (1994) to account for the faunal crash, they suggested that the crash was consistent with a climate-linked contaminant pulse hypothesis wherein dry conditions were the climatic factor linked to the declines. Earlier, Jaeger (1980) had also suggested that drought could adversely impact amphibian populations because dry conditions decreased mobility and reduced foraging success in *Plethodon cinereus*, translating into reduced reproductive output when energy demands for reproduction were not met. Overall, drought and high temperatures are stressful for many amphibians, although drought may be a more influential stressor than elevated temperatures in some areas (e.g., amphibians in Canada; see Ovaska 1997).

Literature focused on hurricane effects on amphibians is very sparse, but data are available for studies that addressed the effects of Hurricane Hugo (September 1989) on the most abundant terrestrial frog in the Luquillo Forest of Puerto Rico, the coqui (*Eleutherodactylus coqui* [Woolbright 1991, 1995]). Adults were not immediately affected, but juveniles experienced substantial mortality after the storm because of an extremely dry post-hurricane period. By October 1990, adult population density increased four-fold over pre-hurricane levels, but adult body size was smaller than pre-hurricane measurements (Woolbright 1991). Increases in adult population size may have been associated with increased availability of adult retreat sites in the understory following the hurricane, because adults used the debris that accumulated in the understory. Although the number of adults in the population increased, reproductive output remained low. Woolbright (1995) showed that juvenile density increased after the adult peak and attributed part of the increase in frog density to a decrease in the density of invertebrate predators.

Ultraviolet radiation

Middleton et al. (2001) attempted to relate satellite-based estimates of surface UV-B to amphibian declines in the New World tropics, and found that UV-B has increased since 1979 at sites where amphibians have declined, particularly in Central America. Solar radiation includes UV radiation (100 to 400 nm), visible light (wavelengths 400 to 770 nm), and infrared radiation (>770 nm). UV radiation that reaches the earth occurs in the wavelengths 295 to 315 nm (UV-B) and 315 to 400 nm (ultraviolet-A [UV-A]). UV intensity is a function of the distance of travel through the ozone layer, thus intensity increases with decreasing solar angle. UV-B is most stable and intense at the equator, but declines with increasing latitude and is most intense at the summer solstice. UV radiation also increases with altitude as reflective atmospheric moisture declines (Caldwell et al. 1980; Caldwell and Flint 1994). Reduction of the thickness of the ozone layer from atmospheric pollution allows more UV-B to reach the earth's surface, and satellite-based estimates of surface UV-B levels have increased by 5% to 10% per decade since 1979, particularly at higher latitudes and in early spring (Herman et al. 1999). Transient increases in UV-B flux in excess of 20% have been observed, although such changes are short (1 to 3 days) and affect a limited area (Middleton et al. 1999). UV-B is of concern because it induces oxidative reactions that interfere with intracellular functions (Smith et al. 2000) and it induces pyrimidine dimer formation in nucleic acids, resulting in impaired transcription (Hays et al. 1996). UV-B may also interact with some chemicals, making them more toxic (see Chapter 4).

Most amphibians have a number of ways to minimize UV damage. Tolerance to UV-B exposure can be mediated in part by the efficiency of photorepair mechanisms for DNA damage. For example, the enzyme photolyase is induced by exposure to sunlight, with the magnitude of induction depending on the duration of exposure. Photolyase activity varies among species and has been suggested to correlate with UV-B sensitivity (Blaustein et al. 1999; Smith et al. 2000). Photoprotection is also provided by the amount and distribution of melanin in the epidermis (Little et al. 2002). UV-B–tolerant boreal toads (*Bufo boreas*) have a distinct double layer of melanin. Woodhouse's toads (*Bufo woodhousii*) that live in

lower altitude habitats also have double melanin layers, but the melanin in the outer layer is less concentrated. The outer melanin layer of gray treefrogs (*Hyla versicolor*), a UV-sensitive species, is diffused. Melanocytes of tiger salamanders (*Ambystoma tigrinum*), which are highly sensitive to UV-B, are limited and widely dispersed throughout the dermis and epidermis (Little and Fabacher 2003).

Amphibians can also mediate exposure to UV-B by behavior. Cascades frogs (*Rana cascadae*) in Olympic National Park, Washington, U.S.A., breed in small shallow ponds but prefer ponds with high dissolved organic carbon (DOC), which attenuates transmission of UV-B (Adams et al. 2001). Alpine newts (*Triturus alpestris*) in Austria avoid laying eggs in ponds with high UV exposure, and their larvae are able to move away from high UV environments (Nagl and Hofer 1997). However, most species that have declined occupy shady forest environments that filter out UV radiation (Lips 1998, 1999), so increases in UV-B alone are unlikely to cause amphibian declines.

Sensitivity of amphibian embryos to UV-B radiation has been the subject of considerable recent research (see reviews by Licht and Grant 1997, Blaustein et al. 1998, Waldman and Tocher 1998, Corn 2000; and additional papers by Langehelle et al. 1999, Starnes et al. 2000). Several studies have shown increased mortality of embryos exposed to ambient UV-B, compared to protected embryos. These results have led to the hypothesis that increased UV-B may play a role in the decline of some species, especially those that lay eggs in shallow water subjected to solar radiation and that have a poor ability to repair UV-induced DNA damage (Blaustein et al. 1998).

Although the sensitivity of early life stages of amphibians to UV-B was demonstrated in laboratory studies, these studies overestimated their susceptibility because unnatural UV spectra were applied (Worrest and Kimeldorf 1975, 1976) or the duration and intensity of exposure were too great to allow for repair by natural mechanisms (Grant and Licht 1995). Studies in the laboratory using measured field levels have indicated that some species tolerate UV at irradiance levels that exceed that of their habitats (*B. boreas, B. woodhousii*; Little et al. 2002). In contrast, other studies indicate that some species are highly sensitive to UV exposure and exhibit injury from exposure at the upper range of irradiance measured in their habitats (Little and Fabacher 2003). In situ field studies have demonstrated that ambient levels of UV-B could lead to mortality of amphibian embryos (Blaustein, Hoffman, et al. 1994; Blaustein et al. 1995; Hays et al. 1996). However, because most studies fail to link mortality with environmental levels of UV-B radiation, population differences in UV sensitivity or unknown experimental factors might be responsible (Ovaska 1997). Alternatively, laboratory studies may overestimate UV-B effects. For example, Diamond et al. (2002) compared laboratory-derived dose–response relationships of three species of *Rana* to estimated UV-B exposure in wetlands in the upper Midwest of the U.S. and found that 21 of 26 sites (81%) never received the level of UV-B exposure that caused mortality or malformations in controlled experiments, suggesting that nocturnal, shelter-, shade-, and depth-seeking behaviors would reduce actual UV exposures.

Most experimental UV-B studies on amphibians have used embryos as the test subjects. Embryos may be vulnerable to UV-B because they cannot move away from the exposure and lack protective measures, such as integument, to limit damage to DNA in cell nuclei. Females, however, could preferentially deposit eggs in locations that are protected from UV-B. Embryos are convenient subjects because they do not require feeding, develop in a few days, and can be assessed quickly. However, embryos might not be the most relevant developmental stage to examine amphibian susceptibility to UV-B radiation. The relative brevity of the developmental period limits total exposure to UV-B, and embryos of most temperate species are present in spring, well before the peak of UV-B flux at the summer solstice.

Further, measures of UV-B flux at the surface of the water are likely to be a poor index of the dose that aquatic life stages receive. Surface waters vary considerably in the depths to which damaging amounts of UV-B can penetrate, because of variation in concentration of DOC (Schindler and Curtis 1997; Adams et al. 2001; Palen et al. 2002; Peterson et al. 2002). Physical structure of the habitat, including shading by topographic features and both terrestrial and aquatic vegetation, will also affect the amount of UV-B that reaches the organism. Once hatching takes place, behavior largely determines UV-B dose. Laboratory studies in simplified habitats (e.g., Ankley et al. 2000) likely overestimate UV-B effects because larvae are unable to use physical structure or behaviors that can reduce exposure. Several studies have demonstrated increased mortality and rates of deformity in larvae exposed to ambient UV-B (Ankley et al. 2000; Tietge et al. 2001; but see Ovaska et al. 1997; Langehelle et al. 1999). However, larval development requires weeks or even years, and often encompasses the period of peak UV-B flux, so that total UV-B doses to which larvae are exposed in nature may be much greater than for embryos. However, experimental studies of larvae have yet to link mortality to effects on populations (Blaustein and Kiesecker 2002 and references therein).

Multiple factors

If we insist that every outcome has a single cause and fail to test multi-factor hypotheses, we risk delaying comprehension of the problem and may inadvertently point research in an unproductive direction (Hilborn and Stearns 1982) in a field where such errors may result in population and species extinction. Single-factor explanations simply may not be sufficient to explain widespread phenomena. Stallard (2001), Carey et al. (2001), and Laurance (1996) looked for correlations among environmental variables and amphibian declines and did not find a single satisfactory explanation accounting for declines. However, each suggested several interacting mechanisms that may be responsible. Even amphibians in natural communities must deal with numerous potential stressors: They must avoid predators; metamorphose before pond desiccation; and compete for food resources, refugia, and mates. Amphibians typically experience a number of natural factors that can cause stress throughout larval development and adulthood, and the interactions among these factors (competition, predation, hydroperiod) are relatively well studied in basic community ecology (e.g., Wilbur 1972, 1987; Morin 1983; Semlitsch 1987). Environmental perturbations due to human influences, therefore, are additional stresses in a community.

Because all populations exist in habitats that are inevitably influenced by multifarious pressures (Figure 5-1), determining how environmental stressors interact will be necessary to understand their effects on habitats and associated fauna. And then, land managers can strive to develop practices that minimize negative impacts. Multiple factors can interact additively (the effect of both stressors is the sum of the individual effects), antagonistically (the effect of both factors is less than the sum of the individual effects), or synergistically (the effect of both factors together is greater than their additive individual effects). Multifactor studies on clear-cutting and burning may indicate, for instance, that amphibians persist on sites that have been only clear-cut (as found in Chazal and Niewiarowski 1998) or only burned, but that the practice of both activities combined reduces survival dramatically. Such a study would help land managers promote amphibian recovery. Proving the interaction of factors, however, will necessitate rigorous experimentation to establish the necessary links (Alford and Richards 1999).

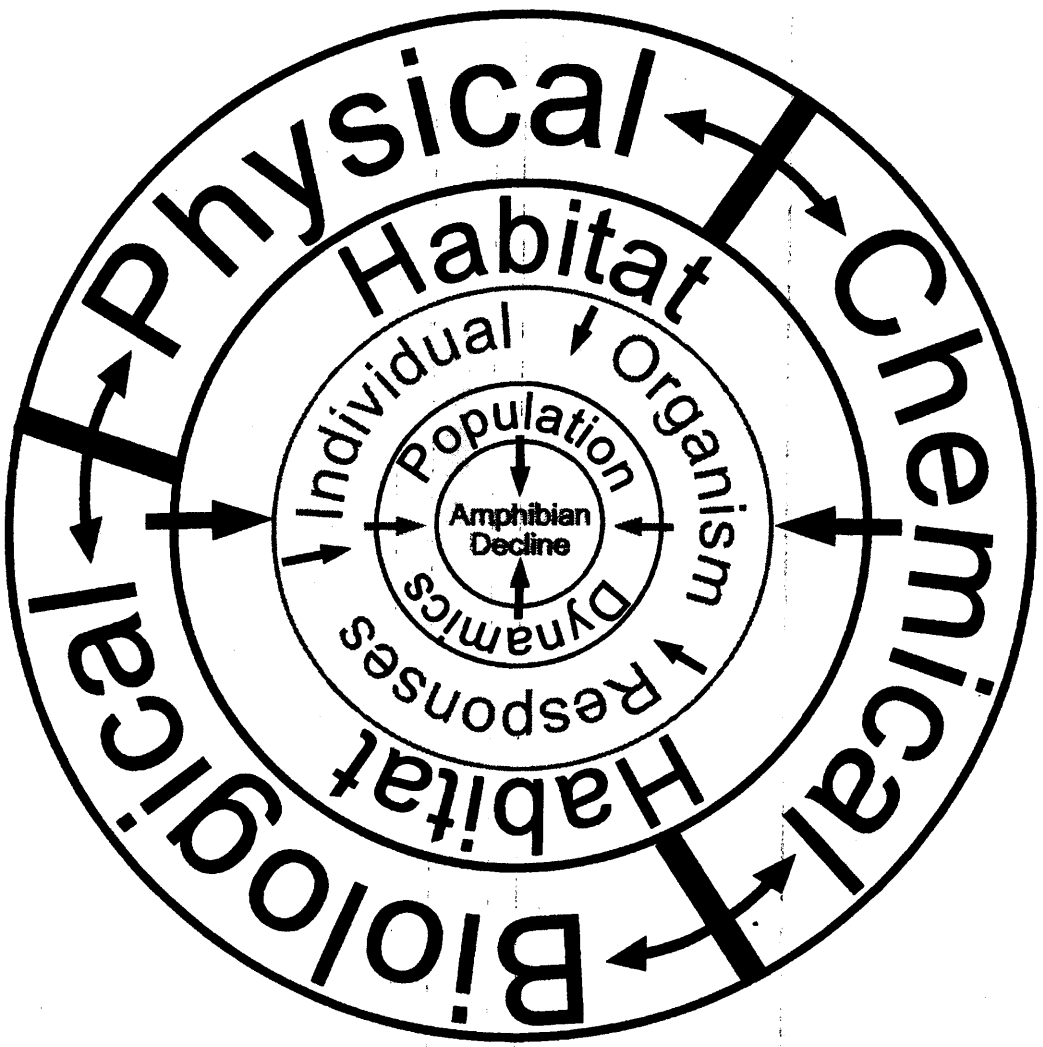

Figure 5-1 Interaction of changes in physical, chemical, and biological environment, as well as in habitat, influencing response of individual organisms, affecting population dynamics, and determining population growth or decline

Kiesecker, Blaustein, and Belden (2001) suggested that high infection rates in the boreal toad (*B. boreas*) by a pathogenic water mold (*Saprolegnia ferax)* were caused by a complex interaction of physical and biotic factors. Boreal toad embryos were previously shown to be susceptible to *Saprolegnia* only in the presence of UV-B radiation (Kiesecker and Blaustein 1995). It was hypothesized that *Saprolegnia* infections killed a higher percentage of larvae in years with low winter precipitation, causing embryos to develop in shallower water with heightened levels of UV-B. They stated that the infection was linked to global climate changes that result from increased UV-B exposure due to shallower pond depth, thereby suppressing immune function and allowing the fungus to infect and kill embryos. Although their results suggested that there was an effect on embryo mortality due to *Saprolegnia* infection with decreasing water depth and with exposure to ambient UV radiation, the assumption that toad embryos are exposed to higher doses of UV-B in dry years is difficult to prove. UV radiation exposure is highly variable among breeding sites due to sources of variation that include seasonal UV-B flux and water chemistry (Corn and Muths 2002; Palen et al. 2002). Demographic modeling suggests that increases in mortality of adult boreal toads is much more important in determining population growth rate than in mortality of other life stages (Biek et al. 2002). On the other hand, one may posit that the mortality induced from UV-sensitive animals may be trivial in comparison to mortality resulting from competition or predation. Alternatively, mortality that affects only some individuals or some clutches may actually have positive effects on the population if individuals that do survive are of better quality (e.g., larger size), similar to the ameliorative effects of predation on prey populations (Morin 1983).

Certainly the work of Kiesecker, Blaustein, and Belden (2001) and others provides a framework to begin hypothesis testing. For instance, determining if embryo mortality from UV results in changes in abundance at the population level or if UV exposure represses immune function and increases susceptibility to a biological disease are feasible steps in relating the stressors to changes in population size and community processes. The conjectures of Kiesecker, Blaustein, and Belden (2001) also point to the importance of examining complex interactions.

Because many abiotic factors are interdependent, a change in one physical factor may cause a cascade of changes. Interactions among water quality parameters have been demonstrated for pH, aluminum concentration, alkalinity, and total cations (Rowe and Dunson 1993), factors that could strongly affect amphibians that require aquatic environments during some portion of their life cycle. Further, clear-cutting timber will change a number of abiotic factors, including local microclimate, soil moisture, and ground temperature (as found in Waldick et al. 1999), and many researchers have demonstrated that amphibian abundance varies with abiotic conditions associated with habitat characteristics (e.g., Stewart 1995; Marsh and Pearman 1997; Block and Morrison 1998; Williams and Hero 2001). Changes caused by habitat destruction can be further compounded by burning and pesticide application. Populations that survive the initial environmental insult are likely, if not typically, exposed to a barrage of other factors that may compromise their persistence.

The amount of UV exposure to amphibians is influenced by a number of factors as well. Increasing temperatures, which can impact amphibian growth, development, and physiology, are associated with decreases in dissolved organic carbon, permitting increased penetration of UV radiation (Scully and Lean 1994; Schindler et al. 1996; Schindler and Curtis 1997; Ovaska 1997; McCarty 2001). Long et al. (1995) have demonstrated that increasing UV levels can significantly reduce survival of northern leopard frog *(Rana pipiens)* embryos under low pH conditions. If UV radiation exposure proves important to amphibian declines, as some suggest, then increased temperatures via global warming may make amphibians more susceptible to UV exposure and may have negative effects on species or individuals with low UV tolerance. Associations between changes in global climate and UV radiation suggest that changes in one factor will also influence the other (see Ovaska 1997) and could degrade the physiological conditions of larvae, juveniles, and adult amphibians.

Anthropogenic changes in the physical and biological environment may occur simultaneously and interact synergistically. The widespread distribution of contaminants in the environment makes their presence increasingly likely in many communities. Contaminants persist and occur in areas beyond their initial place of application, moving geographically via wind currents, water vapor, and rivers even to remote polar regions (reviewed in Van Dijk and Guicherit 1999), and contaminants have been correlated with amphibian declines in California, U.S.A. (Sparling et al. 2000; Davidson et al. 2001). Although chemicals may be present only at sublethal levels, they can alter amphibian communities under a number of biological and physical conditions (Boone and Semlitsch 2001, 2002; Bridges and Boone 2003). Natural levels of UV radiation can influence the fate of chemicals, and increasing UV levels would likely exacerbate problems. Toxicological studies have shown that presence of UV light can increase the potency of chemicals (Ankley et al. 1998; Zaga et al. 1998; Little et al. 2000; Little and Bridges 2001; Bridges et al. 2003) and occasionally decrease their toxicity (Little and Bridges 2001; Bridges et al. 2003). Polycyclic aromatic hydrocarbons (PAHs) and other components of crude and refined petroleum increase toxicity for fish by as much as 10 000 fold in the presence of UV (Oris and Geisy 1987). Further, UV radiation may change the chemical structure of the substance to a more toxic form of that substance. UV radiation breaks down ferrocyanide compounds to release free cyanide, which is toxic to fish and amphibians (Burdick and Lipschuetz 1950; Calfee and Little 2003). Thus, photosensitization can occur at solar irradiance levels that would be otherwise harmless.

The relationship between habitat and climate are so intertwined that it is difficult, and perhaps unrealistic, to try to separate their effects (Aber et al. 2001; Hansen et al. 2001). Changes in environmental climate can alter habitats particularly at the margins of the range by altering the role of occurrences such as fire (Dale et al. 2001). The effects of fire, which is predicted to become more frequent in some environments due to drier summers (Aber et al. 2001), may change species distributions more immediately than the effects of global climate changes alone (Dale et al. 2001). Changes in climate are also predicted to influence outbreaks of pathogens (Alexander and Eischeid 2001; Dale et al. 2001), which could be significant given the concern over their role in many amphibian declines (reviewed in Crawshaw 2000; see Chapter 6). Further, invasive species

may have an advantage during times of habitat transformation resulting from climatic changes and may increase their range to the detriment of native amphibian species that may be less competitive, particularly if the physical environment is testing their physiological limits. Some evidence suggests that exotic species (i.e., fish) have contributed to the spread of pathogens to which amphibians are susceptible (Kiesecker, Blaustein, and Miller 2001).

Overall, the interactions of stressors are poorly understood with respect to their role in influencing amphibian population size and growth rate. It is becoming increasingly clear that analysis of multiple stressors is necessary for evaluation of the potential causes of amphibian declines because amphibians in the wild typically encounter complex environmental conditions influenced by human activities.

Conclusion

The problems of habitat destruction and alteration often have straightforward solutions (i.e., "don't do it") that are typically viewed as not possible, not desirable, or both. Minimizing habitat destruction, maximizing protection of aquatic and terrestrial habitats, and maintaining connectivity among populations would go a long way toward sustaining current levels of biodiversity. However, the apparent widespread incidence of declines whose causes are unclear forces us to realize that the situation is more complex and will require solutions beyond remedies of "do" or "don't do" something. Consequences of global warming are upon us, although the data determining whether we are experiencing natural fluctuations or anthropogenic effects are quite possibly centuries away. Solutions to global change including climate change and increased UV radiation are even more complex, although attempting to reduce carbon dioxide emissions individually, nationally, and internationally through personal and national commitments would be a move in the right direction to limiting environmental changes that damage the ozone layer and biota. The effects and solutions to physical stressors outlined in this chapter will not be quick fixes, but will require sustained support and commitment.

Choice of management options and effectiveness of actions will depend critically upon reliable estimates of demographic rates. Long-term demographic data cannot be merely characterized as a scientific luxury that we are unlikely to obtain. Conservation and management efforts directed at "head-starting" sea turtles proffer a powerful example. "Head-starting" programs helped augment the number of hatchling sea turtles and proceeded for many years (and are still ongoing in some cases) before it became clear through simple demographic analysis that this would likely be ineffective in stabilizing or reversing population declines because high adult survival (rather than high hatchling survival) is critical to maintain population persistence (Frazer 1992; Heppell et al. 1996). Methods for demographic analysis are becoming more sophisticated and also more accessible (see Heppell et al. 2000 for an example and review). However, these tools have not been used in estimating the effects of potential threats to amphibian populations (e.g., UV-B, parasites; but see Biek et al. 2002).

Ultimately, however, the lack of certainty about the roles of physical stressors on amphibian declines described above can be traced to lack of demographic data for specific populations of interest and amphibians in general, and to current limitations in population dynamics theory. For example, boreal toad eggs, collected from a breeding site in the central Oregon Cascade Range and exposed to UV-B and the fungus *Saprolegnia* under laboratory conditions, had a 20% to 25% lower hatching success rate compared to controls (Kiesecker and Blaustein 1995). Although the increased mortality rate of eggs is obvious under laboratory conditions, the consequences of increased mortality for the population growth rate remain unclear. This uncertainty is not necessarily a limitation of the study, per se, but it is a definite limitation of the inferences that can be drawn about population-level consequences. Without life-table data, we cannot estimate population growth rate or determine whether declining populations result from increased death rate or other life-table functions, such as decreased fecundity.

Finally, even with an extensive demographic database, predictions about population consequences will be limited in reliability by theory and how we apply theory. Because many amphibian populations apparently belong to metapopulations (Green 1997; Alford and Richards 1999), intensive studies at single sites (i.e., long-term mark–recapture studies) are unlikely to provide reliable predictions for population dynamics. While it is true that the dynamics of local populations may be driven by metapopulation processes, it is wrong to conclude that intensive studies of single populations may be unnecessary (Alford and Richards 1999). Metapopulation models may focus on patterns of presence–absence in patches across a landscape, but they implicitly include assumptions regarding within-patch demographics (e.g., usually incorporate simple rules about reproductive rates and carrying capacity), which is precisely the kind of data generated by mark–recapture studies. If we abandon detailed studies of individual sites and employ estimates of demographic rates for use in the metapopulation models, then how can we have confidence that the predictions of presence or absence of populations across a landscape are reliable or accurate? The suggestion that metapopulation processes must be incorporated into research on amphibian declines is important, but we must realize that more, not less, data will be required.

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