



## Climate change and amphibian declines: is there a link?

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**Abstract.** Global climates have been changing, sometimes rapidly and dramatically, throughout the evolutionary history of amphibians. Therefore, existing amphibian species have been derived from those that have survived major climatic disturbances. Although recent global climate change has resulted in warming in many regions, temperatures in some areas to date have not changed measurably, or have even cooled. Declines of some amphibian populations have been correlated with climate events, but demonstrations of direct causal relationships need further research. Data are available indicating some indirect effect of climate change on the initiation of breeding activities of some amphibians that

occur earlier than in previous springs, but the costs and benefits of these changes are just beginning to be investigated. Climate may also play an indirect role in facilitating epidemics of infectious disease. Regardless of the role that climate changes may have played in past and current amphibian declines, future shifts in climate, should they prove as dramatic as predicted, will certainly pose challenges for surviving amphibian populations and for successful recovery efforts of species that have suffered declines.

**Key words.** Amphibians, amphibian breeding, amphibian population declines, climate change, El Niño.

### INTRODUCTION

Among the various factors proposed as causes for amphibian population declines, global climate change has received relatively little attention (cf. Linder *et al.*, 2003). Recent studies have linked declines of amphibian populations to variations in temperature and moisture caused by ‘climate change’ in general or by the El Niño phenomenon specifically (Corn & Fogleman, 1984; Heyer *et al.*, 1988; Weygoldt, 1989; Ingram, 1990; Pounds & Crump, 1994; Laurance, 1996; Pounds *et al.*, 1999; Kiesecker *et al.*, 2001). In many cases, these studies have correlated amphibian disappearances with climatic factors over short time periods, including a single climate event. The goal of this paper is to review the strength of the evidence concerning whether global

climate changes have served as direct (the actual cause of death) or indirect (contributory factor that facilitates the direct cause of death) causes of amphibian declines. To that end, this paper will first review the available evidence concerning how the global climate has changed in the past and how it appears to be changing now.

### GLOBAL CLIMATE CHANGE

Throughout the roughly 350 million years of amphibian evolution (Duellman & Trueb, 1985), climate change has been the rule rather than the exception. Periods of relative stability have been punctuated with dramatic, and sometimes quite abrupt, change (Alley *et al.*, 1997; Lang *et al.*, 1999; Severinghaus & Brook, 1999; Taylor, 1999; Birks & Ammann, 2000).

To gain a perspective as to how the current global climate compares to those in the past, it

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is desirable to have the longest climatological records possible. However, temperature, moisture and wind patterns have been measured with instruments for only several centuries, at best (Jones *et al.*, 2001). The rapidity, frequency, and magnitude of climate changes prior to instrumental records have been estimated using proxy data, which include anecdotes from written archives and scientific analyses of growth rings of trees and stalagmites, cores through glaciers and coral reefs, pollen samples from lake sediments, deep-sea sediment cores and others. Most proxy data do not have the high resolution of instrumental data, but they can be used to estimate variation in large-scale temperature and moisture patterns. The overlap between instrumental records and proxy data have been used to assess the climate information provided by various types of proxy data. In turn, error estimates of the proxy data can be used to gauge the accuracy of climatic patterns for which no instrumental records exist (Jones *et al.*, 2001). A compilation of proxy data on palaeoclimates is available at [www.ngdc.noaa.gov/palaeo/ctl/index.html](http://www.ngdc.noaa.gov/palaeo/ctl/index.html).

While the global climate is assumed to have fluctuated throughout the evolution of living organisms, the most accurate proxy data are available for relatively recent times. Analysis of deep-sea sediment cores indicates that the global climate has undergone almost continuous change over the last 65 million years, from periods of warmth with ice-free poles to intervals of intense cold with the extension of continental glaciers (Zachos *et al.*, 2001). Reconstructions of surface temperatures in the Northern Hemisphere over the last millennium indicate that the 11th and 12th centuries were relatively warm and, in fact, averaged about 0.1 °C below the average for the last 30 years of the 20th century. This period was followed by a cooling trend culminating in a long period of relatively cold temperatures in the 17th century, termed 'the Little Ice Age' (Jones *et al.*, 2001). Abrupt cooling also occurred in the early part of the 19th century. The 20th century was the warmest in the last millennium, with an average of 0.2 °C above the mean temperature of the last 500 years. The most rapid warming in the last millennium occurred in the last 30 years of the 20th century (Jones *et al.*, 2001). Although relatively few proxy and instrumental records are available for the Southern Hemisphere, the data

suggest that temperatures in this region have increased significantly over the last 100 years relative to those between 1600 and 1900 (Jones *et al.*, 2001).

Precipitation patterns, as judged by tree ring chronologies and lake sediments, have also varied considerably over time (Woodhouse & Overpeck, 1998). Intense, short (multi-year), and relatively geographically restricted droughts, such as those in the 1930s and 1950s in the United States, have occurred roughly 1–2 times per century over the last millennium. Extremely severe and geographically widespread multi-decadal droughts, such as a 22-year drought in the late 1500s and a 26-year drought in the late 1200s in the American Southwest, have recurred once or twice every 500 years (deMenocal *et al.*, 2000).

Of particular concern, of course, is the rapid warming that occurred during the latter half of the 20th century and its effects on the biota of the earth. In this century, near surface temperatures rose an average of 0.5 °C, with concurrent changes in precipitation patterns and an increase in the frequency and severity of extreme weather events (Easterling *et al.*, 2000). However, this global average increase is far from uniform: daily minimum temperatures have risen about twice as fast as daily maxima (Easterling *et al.*, 2000) and some regions have experienced cooling rather than warming (Trenberth, 1990; Serreze *et al.*, 2000). As a result, it cannot be assumed that all amphibians have been exposed to global warming.

## EL NIÑO

Because amphibian population declines have been linked to climate changes associated with El Niño (e.g. Kiesecker *et al.*, 2001), this next section will examine how this phenomenon has varied over time.

The El Niño–Southern Oscillation (ENSO) phenomenon results from air–sea interactions in the Tropical Pacific that affect rainfall, temperature, ocean currents and wind patterns both locally and over the entire globe (see References in Glynn, 1988; Trenberth, 1997). The name 'El Niño', meaning Christ Child, was applied first to the modest warming that normally occurs near Peru around Christmas-time, but the term has now come to mean the anomalous warming of most of the equatorial Pacific Ocean that occurs

approximately every 2–7 years. As part of this phenomenon, the normally cold, nutrient-rich waters over the eastern two-thirds of the equatorial (5°N–5°S) Pacific Ocean are replaced with warm, hyposaline, nutrient-deficient surface water. El Niño events begin in late spring and can extend into the spring of the following year. The ‘Southern Oscillation’ is the atmospheric component tied to these oceanic changes, with high pressure over Australia and low pressure over the eastern Pacific Ocean during El Niño events. La Niña, the opposite of El Niño, refers to a situation in which anomalously cold waters cover the surface of the equatorial Pacific Ocean (Trenberth, 1997; Fedorov & Philander, 2000).

The ENSO phenomenon, as judged by variation among growth rings of coral reefs, appears to have been absent or significantly reduced below contemporary levels during the Holocene (7000–5000 years before present; Overpeck & Webb, 2000). ENSO events have occurred frequently from 1500 to the present and the frequency has not varied appreciably since 1800 (Quinn *et al.*, 1987). An analysis of ENSO patterns indicates that El Niños and La Niñas have occurred in about 31% and 23%, respectively, of the years since 1950 (Trenberth, 1997). Proxy data suggest that La Niña events may have occurred more frequently since 1850 than in previous centuries (Jones *et al.*, 2001).

In 1976 a large change in sea surface temperatures in the south-western Pacific resulted in an increase in frequency, duration and intensity of ENSO events compared to patterns in the previous 30 years (Trenberth & Hoar, 1996; Guilderson & Schrag, 1998). The unusual features of the 1982–83 phenomenon were both the extreme deviation of sea surface temperatures and the duration of the effect (Glynn, 1988). While the 1982–83 and 1997–98 events were unprecedented in current records, at least seven strong events, possibly equal to or surpassing the magnitude of these two events, may have occurred since 1500 (Overpeck & Webb, 2000). It is currently an open question whether global warming has contributed directly to the change in patterns and severity of ENSO events since 1976.

Because ENSO events affect biological productivity of the ocean, marine communities experience varying degrees of disruptions, including shifts in geographical distribution of near shore

and benthic organisms, mortality of coral reefs, reproductive failure and starvation of marine seabirds and other predators (Glynn, 1988). However, because temperature and moisture patterns over land are also affected by ENSO events, amphibians and other organisms are likely to experience their effects. Because an ecosystem may take more than 1 year to recover from the damage from a severe ENSO event, a change in the frequency of El Niño and La Niña may cause irreparable changes in some biota.

The foregoing review of the palaeoclimatic data suggests that the survival of amphibians over time has depended more on the ability to track continual climate variations than to adapt to fixed conditions.

## CLIMATE AND THE BIOLOGY OF AMPHIBIANS

### Importance of temperature and water to amphibians

Temperature and moisture are the two most prominent components of climate that impact amphibian biology directly. Amphibian body temperatures are determined primarily by heat exchange with air, water, and/or soil or solar heat gain for species that bask in the sun (Hutchison & Dupré, 1992). Body temperature, in turn, determines biochemical, cellular and physiological rate processes, including metabolism, respiration, excretion, circulation and digestion. Most physiological and biochemical rate processes increase by two- to threefold for every 10 °C increase in body temperature (Rome *et al.*, 1992). Gametogenesis and growth rates of larval and postmetamorphic individuals are temperature-dependent (Beebe, 1995; Carey *et al.*, 2003b). In temperate areas, the increase in air and water temperatures in the spring appear important for initiating certain behaviours, including emergence from hibernation and initiation of reproductive activities, such as male calling (Reading, 1998).

Lethal temperatures have been measured in a number of amphibians from a variety of habitats (Rome *et al.*, 1992). In general, amphibians that are exposed to wide daily and seasonal temperature fluctuations tolerate a wider range of high and low temperatures than species that experience a narrow range of body temperatures

(Snyder & Weathers, 1975). Amphibians rarely, if ever, live at temperatures that approach their upper lethal limits, which are given an operational definition of 'the thermal point at which locomotory activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death' (Cowles & Bogert, 1944). The abilities of larvae of some desert amphibians to tolerate very high body temperatures and metamorphosed amphibians to hibernate at or below freezing require special physiological properties not shared by other amphibians (Brown, 1967; Pinder *et al.*, 1992).

Water availability, rather than temperature, is the key climatic determinant for life in semi-arid regions of the world and the major environmental factor determining amphibian distributions (Duellman, 1999). Amphibian reproduction is probably the most vulnerable of all terrestrial vertebrates to variation in precipitation. Because most amphibians lay eggs in standing water (Duellman & Trueb, 1985), eggs and larvae are particularly vulnerable to desiccation. Annual variation in rainfall can have an effect on the number of eggs laid in a given year (Caldwell, 1987). The amount and timing of precipitation can dramatically affect the yearly reproductive output of an amphibian population. For instance, too much precipitation at critical times during egg/larval development can cause egg and larval mortality (Carey *et al.*, 2003b). Even in years with ample precipitation, some reproductive output can be lost in the smallest, most shallow ponds that dry most rapidly (Rowe & Dunson, 1995). In dry years, lack of residual spring snow pack that supplies meltwater to temporary ponds and the absence of early summer precipitation can cause substantial, if not complete, reproductive failure in some amphibians (Rowe & Dunson, 1993, 1995; Carey *et al.*, 2003b). Total reproductive failure in a single year can cause a severe drop in the population size in short-lived species (Stewart, 1995). Even if sufficient water remains in a breeding pond to sustain until metamorphosis, inadequate precipitation during the time when eggs and larvae are in breeding ponds has a number of indirect effects. Reduction in pond size affects food supply, density of tadpoles, size at metamorphosis and subsequent postmetamorphic effects and the

number and efficiencies of predators (Pearman, 1995). Furthermore, concentration of man-made contaminants by evaporation can have adverse or toxic effects on larvae (Carey & Bryant, 1995). Drying of ponds, however, may have alternative beneficial effects which may, at least in part, offset the negative ones: small ponds are colonized by predators, such as predacious beetle larvae (*Dytiscus* spp.) less frequently than are larger ponds (Pearman, 1995).

Adult survivorship can also be impacted by water availability. The high rates of water loss from the skin and respiratory systems of terrestrial metamorphosed amphibians, coupled with the lack of ability to produce concentrated urine, make them vulnerable to desiccation (Shoemaker *et al.*, 1992). In a prolonged drought, extensive mortality of metamorphosed terrestrial and aquatic amphibians could occur if their behavioural abilities to find moist microclimates for the duration of the drought are exceeded. Even if lethal limits are not reached in a severe drought, survivorship may be reduced because the lack of environmental moisture may limit periods of activity, mobility, ability to evade predators and food supply.

Because temperature and moisture have such pervasive effects on amphibian biology, including reproduction, and because of their limited mobility, amphibians should be relatively vulnerable to the effects of rapid climate change, compared to other terrestrial vertebrates (Donnelly, 1998). However, existing amphibians have descended from ancestors that survived rapid changes in climate. What capabilities have been passed on through generations that allow existing amphibians to tolerate extremes in temperature and moisture? While behaviour, thermal and hydric physiology were studied intensively in the 1960s and 1970s and such topics are considered old-fashioned these days, simple questions pertinent to survival of climate change cannot be answered for most amphibian species: how well can the behaviour and physiology of each species adapt to the effects of climate change? What combinations of temperatures and moisture in nature would prove lethal? Which climatic variables are the key indicators of potential threats to the survival of each species? Are extreme climate events more likely to cause mass mortalities than gradual changes?

## HAVE CLIMATE CHANGES CAUSED AMPHIBIAN DECLINES?

The evidence that populations of some amphibian species have declined worldwide over the last few decades has been reviewed elsewhere (Alford & Richards, 1999; Carey *et al.*, 1999; Daszak *et al.*, 1999; Carey, 2000; Houlahan *et al.*, 2000; Carey *et al.*, 2001). In most cases, declines in population size or even population extinctions have occurred, but in a few instances, entire species are thought to have become extinct (Pounds & Crump, 1994; Pounds *et al.*, 1999). Have climate changes been sufficiently severe to directly cause amphibian deaths of some amphibian populations or to indirectly facilitate some other factor that caused death?

Before reviewing the evidence bearing on the possibility that climate change has directly or indirectly caused amphibian declines, it may be useful to review how causality might be established. It is indeed difficult to determine causal relationships between events, like amphibian declines and environmental factors, such as temperature and precipitation, when other factors in the environment vary concurrently. As noted by McCarty (2001), almost all studies concerning responses of organisms to climate change are based on correlations, rather than on definitive experiments determining causality. Correlations do not prove cause and effect. Causality can be determined in laboratory situations in which all factors except one experimental variable are held constant, but compelling proof of causality in nature is difficult when multiple variables exist and possibly interact. Even so, it is possible to increase the degree of certainty that climate change is a direct or indirect cause of amphibian population declines by employing a variety of approaches.

Most studies cited below are anecdotal accounts of declines in populations of one or more species by investigators who discovered evidence of a mass mortality in the field and noted that the season seemed unusually cold, warm, dry, etc. These anecdotal accounts do not prove a causal relation and, as a 'snapshot' of an event, are the most open to question concerning alternative explanations (Hughes, 2000). However, multiple anecdotes compiled together can contribute importantly to the weight of evidence

concerning the existence of a causal relation (McCarty, 2001; Carey *et al.*, 2003a).

Investigators considering studies on climate change as a potential cause of amphibian declines might consider one or more of the following approaches in order to move beyond simple correlation to a more compelling case for the existence of causality than a simple correlation. Many of these ideas are employed commonly in the field of epidemiology.

1. Make observations at more than one site. Co-occurrence of the same climatic factors with die-offs at more than one site is more compelling proof of a causal link than the co-occurrence at a single site. Alternatively, evaluate whether the same climatic factor and die-offs co-occur at the same site in more than one year.
2. Conduct the study for long enough to ensure that each mass mortality event is correlated with similar climatic conditions. In other words, one mass mortality occurring in a wet, cold year and another in a dry, warm year does not provide compelling evidence of causality.
3. Document the temporal association of the climatic conditions and the mass mortality. To be a potential cause of the mortality, the specified climate conditions must invariably occur either prior to or coincident with the mortality, not afterwards.
4. Look for evidence of a dose-response relationship. If greater climatic anomalies are correlated with higher mortality, and the converse, the possibility of a causal relationship deserves further investigation. Of course, not all dose-response relationships are linear; instead, an amphibian species might be unaffected by temperature until it reaches a threshold.
5. Evaluate the plausibility in the association between climatic factors and a mass mortality event. Does it make sense that a 1 °C average increase in annual air temperatures, for example, could cause mortality of a given population in light of what might be known about the behaviour and thermal biology of that species?

Another factor to be considered in the evaluation of a causal role of climate change in amphibian declines is the dataset used by the investigator. To date, investigators have typically used average maximum air temperatures or average

air temperatures, annual rainfall or monthly rainfall as the variable of choice with which to examine the possibility that climatic variables were associated with an amphibian decline. Although average maximal temperatures were probably chosen in some studies because of the expectation that global warming has occurred at a particular site, daily minima have changed far more dramatically in many locations than have maxima (Easterling *et al.*, 2000). For amphibians that are nocturnally active and stay in burrows during the day, maximal air temperatures may be less meaningful than minimal air temperatures.

A number of issues need to be considered: For geographically widespread species, how many weather stations are adequate to describe what climatic conditions a given species has experienced in the recent past? For a correlation of weather data with the phenology of a single population, how far away can the weather station be from the site to be representative of the actual conditions experienced by the population? Because weather stations do not necessarily occur near breeding sites and patterns do not necessarily agree among weather stations within several miles of each other (Stohlgren *et al.*, 1998), what are the best data to use? The choice of environmental datasets is also critical to determine the degree to which climatic factors are changing relative to the recent past. Global warming is not uniform over the globe and some areas have even experienced cooling (Trenberth, 1990) or no directional change in the past few decades (Alexander & Eischeid, 2001). Therefore, investigators may want to use more than one dataset to be certain about trends in their region.

### **CLIMATE CHANGE AS A DIRECT CAUSE OF AMPHIBIAN POPULATION DECLINES**

For climatic factors to serve as a direct cause of amphibian declines, temperature and/or moisture patterns should be shown to have exceeded the lethal limits of a given population. As yet, no compelling evidence exists that these variables, acting singly or synergistically, have reached lethal levels for any amphibian population.

A number of studies have found a correlation between climatic factors and amphibian declines. Few studies have made the effort to determine

whether the observed climatic factors might have reached lethal levels (direct cause) or facilitated some other factor that caused amphibian deaths (indirect). Heyer *et al.* (1988) proposed that a severe frost was the cause of the extinction of five frog species in Brazil between 1979 and 1982. In another area of Brazil, similar population declines in frog species were attributed to unusually dry winters (Weygoldt, 1989). The correlation between droughts and massive declines of stream-dwelling, rain forest amphibians throughout eastern Australia has been noted by several authors (e.g. Ingram, 1990; Laurance, 1996). Laurance (1996), however, conducted an extensive analysis of temperature and rainfall patterns and concluded that the case for weather causing the amphibian declines was not compelling. Rainfall averaged only 10–30% below normal during the five-year period prior to frog declines, particularly during the wet season (Laurance, 1996). However, dry season rainfall increased at many stations. Lower rainfall during the wet season was unlikely to have caused reproductive failure. Secondly, extinction of montane populations of *Rana pipiens* was also thought to be due to drought (Corn & Fogleman, 1984). Finally, a detailed study on *Eleutherodactylus coqui* and several other species of frogs in Puerto Rico showed that a dramatic population decline in 1983 was correlated with increased number of periods of days with less than 3 mm of rainfall (Stewart, 1995). Although rainfall in 1983 was not significantly lower than the average, the length of the dry periods increased noticeably. Pounds *et al.* (1999) found a correlation between the pattern of dry mist frequency associated in Costa Rican highland forests and the decline and likely extinction of several species of amphibians.

In light of the fact that existing amphibians have descended from ancestors that persisted through major global climate disruptions, it is important for future research to determine whether a normal variation in climate typical of a particular region is sufficient to cause amphibian mortalities, or whether only extreme anomalies (more than one or two standard deviations away from the mean) can cause amphibian population declines.

Climate change has been ruled out as a cause of the decline of the red-legged frog (*Rana aurora draytonii*) that is nearly extinct over much of its

range in California (Davidson *et al.*, 2001). Despite an overall warming in the region of the study of about 3 °C per century, the current vs. historical distributions of the frog are not consistent with predictions that warming climate should cause the greatest declines in the southern part of the range and at lower altitudes. This study was a particularly good example of one that considers several possible explanations for decline of an amphibian species and then systematically evaluates each one.

## INDIRECT EFFECTS OF GLOBAL CLIMATE CHANGE

Indirect effects of climate change on amphibian populations would include factors that cause amphibian mortalities by affecting some factor that then causes mortality. Because space limitations preclude a full review of the many possibilities for indirect effects of climate change, we will focus on only two possibilities: whether climate change has caused alterations in the phenology of breeding in a way that diminishes reproductive success and whether climate change has promoted population declines due to infectious disease. These two subjects were chosen because they have received the most attention of any possible indirect effects.

### Phenology of breeding

Species must breed successfully in order to persist over time. Global climate change could potentially disrupt amphibian breeding if global warming caused amphibians to breed earlier in the spring than in previous years, and population recruitment suffered as a consequence. Several studies have shown that the initiation of breeding (arrival at breeding ponds and/or initiation of calling) of at least some amphibian species track variation in ambient temperature (Reading, 1998; Blaustein *et al.*, 2001). For instance, breeding activity of the common toad (*Bufo bufo*), as judged by the first date of the annual arrival at the breeding ponds over a 19-year period, occurred up to 7 weeks earlier in milder winters than in average or cold winters (Reading, 1998). The general cline in breeding date with latitude in several species of amphibians in the United Kingdom is also taken as support of the idea

that initiation of breeding is one factor of amphibian biology that tracks variation in temperature (Beebee, 1995; Reading, 1998).

Although breeding initiation in some amphibian species appears to be cued to a specific thermal threshold in the spring, studies that have sought a relationship between time of breeding and temperature have found contradictory results. A gradual increase (0.11–0.24 °C per year) over a 17-year period in average maximum temperatures during March and April was matched by progressively earlier breeding in two anurans, *Bufo calamita* and *Rana kl. esculenta*, and three species of salamander (*Triturus* spp.) (Beebee, 1995). The anurans and salamanders were breeding 2–3 weeks and 5–7 weeks earlier, respectively, during the last 5 years of the study relative to the first 5 years of the study. However, breeding of *Rana temporaria* in the same localities did not vary. Amount of rainfall had no significant relationship to the initiation of breeding of any of these species. An examination of the onset of calling by six species of North American amphibians found that four species were breeding 10–13 days earlier, but two other species were not in 1990–99, compared to records for the same species from 1900 to 1912 (Gibbs & Briesch, 2001).

The dates of the initiation of breeding activity of the common toad (*Bufo bufo*) in the United Kingdom did not vary significantly during a 19-year study, although 5 of the earliest recorded breeding years occurred within the last decade (Reading, 1998). In a study of the timing of egg-laying of four species of North American amphibians, only one species at one site was breeding earlier than it did 18 years ago (Blaustein *et al.*, 2001). Unfortunately, no data were provided in either of these two studies showing that environmental temperatures had warmed significantly over the course of the studies.

If subsequent studies show that significant warming in various parts of the world is associated with earlier breeding in some species, detailed study of the consequences is needed. The limited evidence available currently indicates that both benefits and problems may result from early breeding. In years in which *Bufo bufo* breed early in the spring, the larval stage lasts 30 days longer than in late spawning years (Reading & Clarke, 1999) Even so, the tadpoles still metamorphosed

an average of 36 days earlier than in late spawning years. The advantage of early metamorphosis is that the toadlets have increased time to grow and store energy prior to hibernation in the autumn. The disadvantage is that tadpole mortality is greater in early years because the cold temperatures associated with early breeding cause increased mortality (Reading & Clarke, 1999). Adults that breed early in the spring may experience a possible deleterious effect on body condition (Reading & Clarke, 1995).

### Infectious disease

Infectious disease is now recognized as a major direct cause of amphibian declines, particularly in relatively untouched environments, on several continents (Berger *et al.*, 1998; Carey *et al.*, 1999, 2001, Carey *et al.*, 2003a; Daszak *et al.*, 1999). The potential role of global climate in the emergence of new pathogens and increasing the susceptibility of wildlife to infectious diseases will be reviewed in detail in a subsequent paper because of space constraints here.

*Saprolegnia ferax* is a fungus that has been reported causing mortality of amphibian eggs in the Pacific North-west (Blaustein *et al.*, 1994). High mortality of embryos of the western toad (*Bufo boreas*) has been proposed to be due to a cause-and-effect relationship between the El Niño/Southern Oscillation, water depth, ultraviolet-B radiation and infection by a fungus *Saprolegnia ferax* (Kiesecker *et al.*, 2001). Low levels of precipitation during ENSO years caused a decrease in water depth during breeding that led to increased exposure of the eggs to UV-B that, in turn, fostered infection by the fungus. The authors conclude that the pervasive evidence that epidemic disease is causing amphibian declines may be associated with climate change.

A newly described chytrid fungus, *Batrachochytrium dendrobatidis*, has been shown by fulfilment of Koch's postulates to be the cause of geographically widespread declines and extinctions of populations of a number of species (Berger *et al.*, 1998; Nichols *et al.*, 2001). The origin of this particular fungus is unknown; analysis of the molecular structure of *Batrachochytrium* has revealed no close relatives among members of the Phylum Chytridiomycota (James *et al.*, 2000). An analysis of temperature

and moisture anomalies generated from two independent datasets for four areas (north-eastern Queensland, Puerto Rico, central Colorado Rockies, and Costa Rica/Panama) in which amphibian mass mortalities have been attributed to *Batrachochytrium*, found that no extreme climate events occurred just prior to or coincident with the onset of mass mortalities (Alexander & Eischeid, 2001). Additionally, no similarities in weather patterns at the onset of die-offs were evident among the four sites. As a result, the study concluded that climate was not an indirect cause of the outbreaks of this disease.

### FUTURE RESEARCH NEEDS

The recent report of the Intergovernmental Panel on Climate Change confirmed a global mean warming of 0.6 °C during the 20th century and predicted a mean global temperature increase between 1.4 and 4.8 °C between 1990 and 2100 (IPCC, 2001). Changes in rainfall patterns and increasing severity of climate fluctuations are likely along with the increasing temperatures. Even if climate change has not yet caused amphibian declines, amphibians will undoubtedly be affected by these future variations in climate. So little research has been conducted on the topic of climate change and amphibian declines that virtually every facet needs more research. More basic studies are needed on temperature and moisture tolerances and behavioural means of compensating for changes in climate of amphibians in areas where climate changes have already been demonstrated. The current drought in the western and south-western part of the United States should provide excellent opportunities to study how amphibians deal with a dramatic, sudden change in climate. Additionally, we need more information about whether amphibians are changing their distributional patterns in response to defined climate change and how climate change affects reproductive success, availability of prey and incidence of infectious disease. Most importantly, we need to understand interrelations among the rate of change and degree of severity of climate change and amphibian behaviour, physiological properties (tolerances of thermal extremes and dehydration) of various life stages of amphibians, population dynamics, energetics, food supplies, vulnerability of amphibians



to predators and competitors, metapopulation dynamics and population genetic structure. Much more information about the genetics of amphibians is particularly needed: genetic limitations on the rate of adaptation to new environments, coupled with limitations on gene flow by anthropomorphic habitat destruction, are predicted to reduce the rate of adaptation below the rate of future climate change (Lynch & Lande, 1993; Davis & Shaw, 2001).

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## REFERENCES

- Alexander, M.A. & Eischeid, J.K. (2001) Climate variability in regions of amphibian declines. *Conservation Biology* **15**, 930–942.
- Alford, R.A. & Richards, S.J. (1999) Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics* **30**, 133–165.
- Alley, R.B., Mayewski, P.A., Sowers, T., Stuiver, M., Taylor, K.C. & Clark, P.U. (1997) Holocene climatic instability: a prominent, widespread event 8200 yr ago. *Geology* **25**, 483–486.
- Beebee, T.J.C. (1995) Amphibian breeding and climate. *Nature* **374**, 219–220.
- Berger, L., Speare, R., Daszak, P., Green, D.E., Cunningham, A.A., Goggin, C.L., Slocombe, R., Ragan, M.A., Hyatt, A.D., McDonald, K.R., Hines, H.B., Lips, K.R., Marantelli, G. & Parkes, H. (1998) Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proceedings of the National Academy of Sciences* **95**, 9031–9036.
- Birks, H.H. & Ammann, B. (2000) Two terrestrial records of rapid climatic change during the glacial–Holocene transition (14 000–9000 calendar years BP from Europe. *Proceedings of the National Academy of Sciences* **97**, 1390–1394.
- Blaustein, A.R., Belden, L.K., Olson, D.H., Root, T.L. & Kiesecker, J.M. (2001) Amphibian breeding and climate change. *Conservation Biology* **15**, 1804–1809.
- Blaustein, A.R., Hokit, D.G., O'Hara, R.K. & Holt, R.A. (1994) Pathogenic fungus contributes to amphibian losses in the Pacific Northwest. *Biological Conservation* **67**, 251–254.
- Brown, H.A. (1967) High temperature tolerance of the eggs of a desert anuran, *Scaphiopus hammondi*. *Copeia* **1967**, 365–370.
- Caldwell, J.P. (1987) Demography and life history of two species of chorus frogs (Anura: Hylidae) in South Carolina. *Copeia* **1987**, 114–127.
- Carey, C. (2000) Infectious disease and worldwide declines of amphibian populations, with comments on emerging diseases in coral reef organisms and in humans. *Environmental Health Perspectives* **108** (Suppl. 1), 143–150.
- Carey, C., Bradford, D.F., Brunner, J.F., Collins, J.P., Davidson, E.W., Longcore, J.E., Ouellet, M., Pessier, A.P. & Schock, D.M. (2003a) Biotic factors in amphibian declines. *Multiple stressors and declining amphibian populations: evaluating cause and effect* (ed. by G. Linder, D.W. Sparling and S.K. Krest), pp. 00–00. Society of Environmental Toxicology and Chemistry, Boca Raton, FL, in press.
- Carey, C. & Bryant, C.J. (1995) Possible interrelations among environmental toxicants, amphibian development, and decline of amphibian populations. *Environmental Health Perspectives* **103** (Suppl. 4), 13–17.
- Carey, C., Cohen, N. & Rollins-Smith, L. (1999) Amphibian declines: an immunological perspective. *Developmental and Comparative Immunology* **23**, 459–472.
- Carey, C., Corn, P.S., Jones, M.S., Livo, L.J., Muths, E. & Loeffler, C.W. (2003b) Environmental and life history factors that limit recovery. In: *Southern Rocky Mountain populations of boreal toads (Bufo boreas). Status and conservation of North American amphibians* (ed. by M. Lanoo), pp. 00–00. University of California Press, Berkeley, CA, in press.
- Carey, C., Heyer, W.R., Wilkinson, J., Alford, R.A., Arntzen, J.W., Halliday, T., Hungerford, L., Lips, K.R., Middleton, E.M., Orchard, S.A. & Rand, A.S. (2001) Amphibian declines and environmental change: use of remote-sensing data to identify environmental correlates. *Conservation Biology* **15**, 903–913.
- Corn, P.S. & Fogleman, J.C. (1984) Extinction of montane populations of the northern leopard frog (*Rana pipiens*) in Colorado. *Journal of Herpetology* **18**, 147–152.
- Cowles, R.B. & Bogert, C.M. (1944) A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History* **83**, 261–296.
- Daszak, P., Berger, L., Cunningham, A.A., Hyatt, A.D., Green, D.E. & Speare, R. (1999) Emerging infectious disease and amphibian population declines. *Emerging Infectious Diseases* **5**, 735–748.
- Davidson, C., Shaffer, H.B. & Jennings, M.R. (2001) Declines of the California red-legged frog:

- climate, UV-B, habitat, and pesticides hypotheses. *Ecological Applications* **11**, 464–479.
- Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science* **292**, 673–679.
- Donnelly, M.A. (1998) Potential effects of climate change on two neotropical amphibian assemblages. *Climatic Change* **39**, 541–561.
- Duellman, W.E., ed. (1999) *Patterns of distribution of amphibians*. Johns Hopkins University Press, Baltimore, MD.
- Duellman, W.E. & Trueb, L. (1985) *Biology of amphibians*. McGraw-Hill Co., New York.
- Easterling, D.R., Karl, T.R., Gallo, K.P., Robinson, D.A., Trenberth, K.A. & Dai, A. (2000) Observed climate variability and change of relevance to the biosphere. *Journal of Geophysical Research* **105**, 20, 101–20, 114.
- Fedorov, A.V. & Philander, S.G. (2000) Is El Niño changing? *Science* **288**, 1997–2002.
- Gibbs, J.P. & Briesch, A.R. (2001) Climate warming and calling phenology of frogs near Ithaca, New York, 1900–99. *Conservation Biology* **15**, 1175–1178.
- Glynn, P.W. (1988) El Niño–Southern Oscillation 1982–83: nearshore, population, community and ecosystem responses. *Annual Review of Ecology and Systematics* **19**, 309–345.
- Guillemson, T.P. & Schrag, D.P. (1998) Abrupt shift in subsurface temperatures in the Tropical Pacific associated with changes in El Niño. *Science* **281**, 240–243.
- Heyer, W.R., Rand, A.S., da Cruz, C.A.G. & Peixoto, O.L. (1988) Decimations, extinctions, and colonizations of frog populations in southeast Brazil and their evolutionary implications. *Biotropica* **20**, 230–235.
- Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H. & Kuzmin, S.L. (2000) Quantitative evidence for global amphibian population declines. *Nature* **404**, 752–755.
- Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* **15**, 505–515.
- Hutchison, V.H. & Dupré, K. (1992) Thermoregulation. *Environmental Physiology of the Amphibia* (ed. by M.E. Feder and W.W. Burggren), pp. 206–249. University of Chicago Press, Chicago.
- Ingram, G.J. (1990) The mystery of the disappearing frogs. *Wildlife Australia* **27**, 6–7.
- Intergovernmental Panel on Climate Change (IPCC) (2001) *Climate change 2001: the scientific basis*. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (ed. by J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell & C.A. Johnson), pp. 1–879. Cambridge University Press, Cambridge.
- James, T.Y., Porter, D., Leander, C.A., Vilgalys, R. & Longcore, J.E. (2000) Molecular phylogenetics of the Chytridiomycota supports the utility of ultrastructural data in chytrid systematics. *Canadian Journal of Botany* **78**, 336–350.
- Jones, P.D., Osborn, T.J. & Briffa, K.R. (2001) The evolution of climate over the last millennium. *Science* **292**, 662–666.
- Kiesecker, J.M., Blaustein, A.R. & Belden, L.K. (2001) Complex causes of amphibian population declines. *Nature* **410**, 681–684.
- Lang, C., Leuenberger, M., Schwander, J. & Johnson, S. (1999) 10 C rapid temperature variation in central Greenland 70 000 years ago. *Science* **286**, 934–937.
- Laurance, W.F. (1996) Catastrophic declines of Australian rainforest frogs: is unusual weather responsible? *Biological Conservation* **77**, 203–212.
- Linder, G., Sparling, D.W. & Krest, S.K., eds (2003) *Multiple stressors and declining amphibian populations: evaluating cause and effect*. Society of Environmental Toxicology and Chemistry, Boca Raton, FL.
- Lynch, M. & Lande, R. (1993) Evolution and extinction in response to environmental change. *Biotic interactions and global change* (ed. by P.M. Kareiva, J.G. Kingsolver and R.B. Huey), pp. 234–250. Sinauer Associates, Sunderland, MA.
- McCarty, J.P. (2001) Ecological consequences of recent climate change. *Conservation Biology* **15**, 320–331.
- deMenocal, P., Ortiz, P., Guillemson, T. & Sarnthein, M. (2000) Coherent high- and low-latitude climate variability during the Holocene warm period. *Science* **288**, 2198–2202.
- Nichols, D.K., Lamirande, E.W., Pessier, A.P. & Longcore, J.E. (2001) Experimental transmission of cutaneous chytridiomycosis in dendrobatid frogs. *Journal of Wildlife Diseases* **37**, 1–11.
- Overpeck, J. & Webb, R. (2000) Nonglacial rapid climate events: past and future. *Proceedings of the National Academy of Sciences* **97**, 1335–1338.
- Pearman, P.B. (1995) Effects of pond size and consequent predator density on two species of tadpoles. *Oecologia* **102**, 1–8.
- Pinder, A.W., Storey, K.B. & Ultsch, G.R. (1992) Estivation and hibernation. *Environmental physiology of the amphibia* (ed. by M.E. Feder and W.W. Burggren), pp. 250–276. University of Chicago Press, Chicago.
- Pounds, J.A. & Crump, M.L. (1994) Amphibian declines and climate disturbance: the case of the golden toad and harlequin frog. *Conservation Biology* **8**, 72–85.
- Pounds, J.A., Fogden, M.P.L. & Campbell, J.H. (1999) Biological response to climate change on a tropical mountain. *Nature* **398**, 611–614.
- Quinn, W.H., Zopf, D.O., Short, K.S. & Kuo Yang, R.T.W. (1987) El Niño occurrences over the past four and a half centuries. *Journal of Geophysical Research* **92**, 14449–144461.

- Reading, C.J. (1998) The effect of winter temperatures on the timing of breeding activity in the common toad *Bufo bufo*. *Oecologia* **117**, 469–475.
- Reading, C.J. & Clarke, R.T. (1995) The effects of density, rainfall and environmental temperature on body condition and fecundity in the common toad, *Bufo bufo*. *Oecologia* **102**, 453–459.
- Reading, C.J. & Clarke, R.T. (1999) Impacts of climate and density on the duration of the tadpole stage of the common toad *Bufo bufo*. *Oecologia* **121**, 310–315.
- Rome, L.C., Stevens, E.D. & John-Alder, H.B. (1992) The influence of temperature and thermal acclimation on physiological function. *Environmental physiology of the amphibia* (ed. by M.E. Feder and W.W. Burggren), pp. 183–205. University of Chicago Press, Chicago.
- Rowe, C.L. & Dunson, W.A. (1993) Relationships between abiotic parameters and breeding effort by three amphibians in temporary wetlands in central Pennsylvania. *Wetlands* **13**, 237–246.
- Rowe, C.L. & Dunson, W.A. (1995) Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of central Pennsylvania, USA. *Oecologia* **102**, 397–403.
- Serreze, M.C., Walsh, J.E., Chapin, F.S., III, Osterkamp, T., Dyurgerov, M., Romovsky, V., Oechel, W.C., Morison, J., Zhang, T. & Barry, R.G. (2000) Observational evidence of recent change in the northern high-latitude environment. *Climatic Change* **46**, 159–207.
- Severinghaus, J.P. & Brook, E.J. (1999) Abrupt climate change at the end of the last glacial period inferred from trapped air in polar ice. *Science* **286**, 930–933.
- Shoemaker, V.H., Hillyard, S.D., Jackson, D.C., McClanahan, L.L., Withers, P.C. & Wygoda, M.L. (1992) Exchange of water, ions, and respiratory gases in terrestrial amphibians. *Environmental physiology of the amphibia* (ed. by M.E. Feder and W.W. Burggren), pp. 125–150. University of Chicago Press, Chicago.
- Snyder, G.K. & Weathers, W.W. (1975) Temperature adaptations of amphibians. *American Naturalist* **109**, 93–101.
- Stewart, M.M. (1995) Climate driven population fluctuations in rain forest frogs. *Journal of Herpetology* **29**, 437–446.
- Stohlgren, T.J., Chase, T.N., Pielke, R.A., Kittel, T.G.F. & Baron, J.S. (1998) Evidence that local land use practices influence regional climate, vegetation, and stream flow patterns in adjacent natural areas. *Global Change Biology* **4**, 495–505.
- Taylor, K. (1999) Rapid climate change. *American Scientist* **87**, 320–327.
- Trenberth, K.E. (1990) Recent observed interdecadal climate changes in the Northern Hemisphere. *Bulletin of the American Meteorological Society* **71**, 988–993.
- Trenberth, K.E. (1997) The definition of El Niño. *Bulletin of the American Meteorological Society* **78**, 2771–2777.
- Trenberth, K.E. & Hoar, T.J. (1996) The 1990–95 El Niño–Southern Oscillation event: longest on record. *Geophysical Research Letters* **23**, 57–60.
- Weygoldt, P. (1989) Changes in the composition of mountain stream frog communities in the Atlantic mountains of Brazil: frogs as indicators of environmental deteriorations? *Studies on Neotropical Fauna and Environment* **243**, 249–255.
- Woodhouse, C.A. & Overpeck, J.T. (1998) 2000 years of drought variability in the Central United States. *Bulletin of the American Meteorological Society* **79**, 2693–2714.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**, 686–687.