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Climate change and amphibians

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Abstract

Amphibian life histories are exceedingly sensitive to temperature and precipitation, and there is good evidence that recent climate change has already resulted in a shift to breeding earlier in the year for some species. There are also suggestions that the recent increase in the occurrence of El Nio events has caused declines of anurans in Central America and is linked to elevated mortality of amphibian embryos in the northwestern United States. However, evidence linking amphibian declines in Central America to climate relies solely on correlations, and the mechanisms underlying the declines are not understood. Connections between embryo mortality and declines in abundance have not been demonstrated. Analyses of existing data have generally failed to find a link between climate and amphibian declines. It is likely, however, that future climate change will cause further declines of some amphibian species. Reduced soil moisture could reduce prey species and eliminate habitat. Reduced snowfall and increased summer evaporation could have dramatic effects on the duration or occurrence of seasonal wetlands, which are primary habitat for many species of amphibians. Climate change may be a relatively minor cause of current amphibian declines, but it may be the biggest future challenge to the persistence of many species.

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Abstract
Climate change and amphibians.— Amphibian life histories are exceedingly sensitive to temperature and precipitation, and there is good evidence that recent climate change has already resulted in a shift to breeding earlier in the year for some species. There are also suggestions that the recent increase in the occurrence of El Niño events has caused declines of anurans in Central America and is linked to elevated mortality of amphibian embryos in the northwestern United States. However, evidence linking amphibian declines in Central America to climate relies solely on correlations, and the mechanisms underlying the declines are not understood. Connections between embryo mortality and declines in abundance have not been demonstrated. Analyses of existing data have generally failed to find a link between climate and amphibian declines. It is likely, however, that future climate change will cause further declines of some amphibian species. Reduced soil moisture could reduce prey species and eliminate habitat. Reduced snowfall and increased summer evaporation could have dramatic effects on the duration or occurrence of seasonal wetlands, which are primary habitat for many species of amphibians. Climate change may be a relatively minor cause of current amphibian declines, but it may be the biggest future challenge to the persistence of many species.

Key words: Amphibians, Amphibian decline, Breeding phenology, Global climate change.

Resumen
Cambio climático y anfibios.— Las historias vitales de los anfibios son sumamente sensibles a la temperatura y a la precipitación, y hay una clara evidencia que el reciente cambio climático ha tenido como resultado para algunas especies una anticipación del periodo de cría a lo largo del año. También se cree que el aumento reciente en la ocurrencia de fenómenos de El Niño ha causado el descenso de anuros en América Central y está relacionado con la mortalidad elevada de embriones de anfibios en el noroeste de los Estados Unidos. Sin embargo, la evidencia que relaciona el descenso de anfibios en América Central con el clima está basado únicamente en correlaciones, y no se entienden los mecanismos fundamentales que provocan este descenso. No se han podido demostrar las conexiones entre la mortalidad de embriones y el descenso de abundancia. El análisis de los datos generalmente falla a la hora de encontrar una conexión entre descensos de anfibios y el clima. Es probable, sin embargo, que posteriores cambios climáticos puedan causar descensos adicionales de algunas especies de anfibios. La humedad reducida de la tierra podría reducir las especies presa y eliminar el habitat. La reducción de nevadas invernales y el incremento de la evaporación en verano podrían tener efectos dramáticos en la duración u ocurrencia de pantanos estacionales, que es el habitat principal para muchas especies de anfibios. El cambio del clima puede ser una causa relativamente secundaria de los descensos actuales de anfibios, pero en el futuro puede ser el desafío más grande a la persistencia de muchas especies.

Palabras clave: Anfibios, Descenso de anfibios, Fenologia de cría, Cambio climático global.

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Introduction

Considerable progress has been made in the past decade in documenting the nature and extent of amphibian declines (Waldman & Tocher, 1998; Alford & Richards, 1999; Corn, 2000; Houlahan et al., 2000; Hero & Shoo, 2003). Declines of amphibian species have been documented in most of the world, including Spain (Márquez et al., 1995; Bosch et al., 2001; Martínez–Solano et al., 2003). Knowledge of the status of amphibians is incomplete, but it appears that declines are most severe in Australia (Laurence et al., 1996), Central America (Pounds et al., 1997; Lips, 1998, 1999), and the western United States (Drost & Fellers, 1996; Fisher & Shaffer, 1996; Sredl et al., 1997). There is also a better understanding of at least some of the causes of amphibian declines, compared to 1990, when the issue of declining amphibians first gained widespread attention (Collins & Storfer, 2003). Habitat destruction or alteration, contaminants, introduced predators, and disease have all been identified as potential or likely causes of declines (Stebbins & Cohen, 1995; Sparling et al., 2000; Linder et al., 2003; Semlitsch, 2003). Global change as a cause of amphibian declines has also been studied from two main perspectives: increasing temperatures and increasing ultraviolet–b radiation (UV–B) due to thinning of stratospheric ozone. Although field and laboratory experiments have shown that ambient UV–B may cause mortality or deformities in some amphibian species (Blaustein et al., 1998; 2003b), the UV–B hypothesis is controversial and has been the subject of a series of contentious critiques and rebuttals (Licht & Grant, 1997; Corn, 2000; Cummins, 2002; Kats et al., 2002; Blaustein et al., 2003b, 2004; Blaustein & Kats 2003; Licht, 2003). Support for the hypothesis that increasing UV–B has contributed to amphibian declines is undermined by a lack of evidence linking results from experimental studies to changes in abundance or distribution (Corn & Muths, 2002) and by the general lack of evidence that amphibians have been exposed to increased doses of UV–B (Corn & Muths, 2004).

There is increasingly strong evidence, however, that recent climate change has affected the biology of numerous species worldwide. Global average temperature has increased by about 0.6°C during the past century, which is the warmest period of the preceding millennium (Jones et al., 2001). This increase in temperature is largely attributable to increasing greenhouse gasses (Crowley, 2000). Warming spring temperatures have resulted in measurable shifts in phenology (e.g., timing of budding, flowering, emergence, breeding) to earlier dates, and distributions of some plants and animals have shifted pole–ward and higher in elevation (Walther et al., 2002; Parmesan & Yohe, 2003; Root et al., 2003). The effects on amphibians observed so far mainly involve changes in the timing of breeding of some species (Blaustein et al., 2003a; Carey & Alexander, 2003), and not changes in distribution. For example, Livo & Yeakley (1997) failed to detect any directional change in elevation associated with declines of Boreal Toads (*Bufo boreas*) in the Rocky Mountains in Colorado, USA. However, Martínez–Solano et al. (2003) attributed the increase in occurrence of Iberian Green Frogs (*Rana perezi*) in Peñalara National Park in Spain to recent climate warming. Thomas et al. (2004) estimated changes in distribution for a number of species based on predicted changes in their climate envelopes, and by applying the relationship between area and diversity, predicted that 18–35% of the species they examined (which included 23 frogs from Queensland, Australia) will have a high risk of extinction by 2050. Because amphibian decline is already a significant problem, the potential for greatly increased risk of extinction makes it important to understand how climate change affects amphibians.

Amphibians are ectotherms, and all aspects of amphibian life history are strongly influenced by the external environment, including weather and climate. Temperature is a particularly important factor affecting aquatic amphibian larvae. Ultsch et al. (1999) provided a concise statement:

"…environmental temperature dramatically affects the time taken to reach metamorphosis, which can be critical to the survival of an individual faced with a drying habitat or the onset of winter. Temperature also affects differentiation and growth rates, body size at metamorphosis, mechanisms of gas exchange, rates of energy metabolism, and undoubtedly many other physiological parameters documented in ectothermic vertebrates. Moreover, the limits of temperature tolerance and temperature–dependent life history traits of anuran larvae are generally related to the geographic distribution of a species."

Ovaska (1997) and Donnelly & Crump (1998) described how changes in temperature and precipitation regimes could result in changes in the distribution and abundance of amphibian populations. Direct effects include changes in movements, phenology, and physiological stress. Indirect effects include changes in predators, competitors, food supply, and habitat. Most research to date has emphasized direct effects of climate change. Indirect effects, particularly the links to population dynamics, are notoriously difficult to document.

The consequences of climate change are diverse, and effects can be beneficial as well as detrimental (Ovaska, 1997; McCarty, 2001). A shift in breeding activity to earlier in the season may provide additional time for growth and development. Larger individuals may survive over winter better and may have increased reproductive fitness than small ones (Reading & Clarke, 1999). Breeding earlier reduces exposure to UV–B (Merilä et al., 2000; Corn & Muths, 2002; Cummins, 2003). On the other hand, earlier breeding could bring increased risk of exposure to extreme temperatures

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from more variable early spring weather (Corn & Muths, 2002). The effects of changes in temperature and precipitation on hydrology and hydroperiod (the length of time a temporary pond retains water) may have large effects on amphibians. Early drying of temporary ponds may result in less time available to complete metamorphosis (Semlitsch, 1987; Pechmann et al., 1989, Rowe & Dunson, 1995). Changes in breeding phenology and pond hydrology may affect growth rates of larvae (Rowe & Dunson, 1995; Reading & Clarke, 1999; Boone et al., 2002), and because much predation on amphibian larvae is related to size, this may alter the relationships between amphibians and their predators.

Several recent papers have reviewed the effects of climate change on amphibians (Blaustein et al., 2003a; Boone et al., 2003; Carey & Alexander, 2003). However, few studies have addressed the effects of climate change on amphibians in montane or boreal habitats with persistent winter snow cover, where the timing of snowmelt is the primary influence on breeding phenology. Thomas et al. (2004) predicted the smallest increase in extinction risk in alpine and boreal forest habitats, but warming temperatures in the next 50–100 years are predicted to drastically alter the characteristics of mountain snow packs. Numerous questions still need answers if we are to predict how climate change will affect the distribution and abundance of amphibians.

Effects of climate change on amphibians

Changes in breeding phenology

Several studies have demonstrated trends towards breeding earlier by some species of amphibians. Terhivuo (1988) used the longest time series for amphibians, 140 years of observations collected by volunteers in Finland, and found that Common Frogs (*Rana temporaria*) bred 2 to 13 days earlier in the 1980s than in the 1840s, depending on latitude. Gibbs & Breisch (2001) compared data on the dates of first calling by anurans near Ithaca, NY collected 1900–1912 (Wright, 1914) to data gathered by the during 1990–1999 by the New York State Amphibian and Reptile Atlas Project. Four species began breeding activity significantly earlier (by 10–14 days) during the last decade, compared to the first 12 years of the 20th Century. Over the same period, significant increases in mean daily temperatures (1.2–2.3°C) also occurred in 5 of the 8 months important to gametogenesis in these species. In Poland, the dates of first spawning by *R. temporaria* and Common Toads (*B. bufo*) shifted 8–9 days earlier between 1978 and 2002 and were correlated with warmer spring temperatures (Tryjanowski et al., 2003). The most dramatic shifts in the shortest time were found in England, where two anuran species deposited eggs 2–3 weeks earlier and the three species of salamander arrived at breeding ponds 5–7 weeks earlier in 1990–1994 compared to 1978–1982 (Beebee, 1995). These changes result from warmer spring temperatures associated with the North Atlantic Oscillation (Forchhammer et al., 1998).

The trend toward earlier breeding by amphibians in recent years is not universal. There are about an equal number of cases in England and North America where there is no significant trend toward earlier breeding as there are cases of significant trends (Beebee, 1995; Reading, 1998; Blaustein et al., 2001; Gibbs & Breisch, 2001; Corn & Muths, 2002). Most of these cases use time series of < 20 years, which may be too short to demonstrate significant trends in the face of large interannual variation in the timing of breeding. For example, Blaustein et al. (2001) found a non–significant trend toward earlier breeding in one of three populations of *B. boreas* in the Cascade Mountains in Oregon, USA for 1982–1999. Corn (2003) analyzed these data using the relationship between the timing of breeding and the size of the winter snow pack to model the timing of breeding. Predicted breeding in the one population showed a much more pronounced trend toward breeding earlier by about 20 days between 1950 and 2000.

Long time series (>50 years) are probably necessary to separate the effects of anthropogenic warming from multi–decadal cycles on changes in breeding phenology. That Beebee (1995) and Tryjanowski et al. (2003) found greater shifts in phenology after about 30 years than did Terhivuo (1988) after 140 years may reflect this phenomenon. For example, snow accumulation in the northwest United States is strongly influenced by the Pacific Decadal Oscillation (PDO), Selkowitz et al., 2002). Because the 1950s were a period of higher than average snowfall, the trend toward earlier breeding by the population of *B. boreas* in Oregon (Corn, 2003) is likely to have been strongly influenced by the PDO.

Changes in populations

Climate change has been considered a potential cause of population declines since the beginning of the current spate of concern about the status of amphibians (Wyman, 1990), but the role of climate change in the decline of anurans in the cloud forest of Costa Rica has received the most attention. About half of the 50 species expected to occur in the Monteverde region had disappeared by 1990 (Pounds et al., 1997). These included the distinctive Golden Toad (*B. periglenes*). The decline of this species was first observed in 1987, and is not been observed since 1989 and is likely extinct (Crump et al., 1992). Pounds & Crump (1994) described the 1987 crash of *B. periglenes* as resulting from above average temperatures and below average precipitation that were associated with a strong El Niño/ Southern Oscillation (ENSO). This event killed eggs and tadpoles by premature drying of breeding ponds, but the explanation for the subsequent disappearance of adult toads was not apparent. Pounds and

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Crump discussed hypotheses for how adults may have been affected, including physiologic stress, impaired immune system function leading to disease, and contaminants. They also described the decline of the Harlequin Frog (*Atelopus varius*) in the same region. This species congregates in moist refugia, such as the splash zones of waterfalls, during dry periods, and becomes more susceptible to predation and parasitism (Pounds & Crump, 1987; Donnelly & Crump, 1998).

Pounds et al. (1999) described continuing population fluctuations of anurans at Monteverde in the 1990s, with significant declines involving about 20 species in 1994 and 1998. These more recent declines were also correlated with warm and dry conditions associated with decreasing dry season mist frequency. The retreat of the cloud bank to higher elevations is a product of global warming and is accentuated during strong ENSO events (Still et al., 1999). Pounds et al. (1999) also observed changes in other animals, in addition to declines of anurans. In a cloud–forest study plot, there has been an increase in the frequency of bird species that normally breed at lower elevations below the cloud forest, and two species of anoline lizards, endemic to the highlands of western Costa Rica and Panama, declined and disappeared by 1996. Although the changes in the cloud forest fauna were strongly correlated with climatic events, our understanding of the mechanisms underlying the declines of anurans and lizards has not progressed beyond the hypotheses presented by Pounds et al. (1997). Middleton et al. (2001) used satellite–based observations to estimate surface UV–B exposure at Central and South American sites, including Monteverde, where amphibian declines have been observed. They found increasing trends from 1979 to 1998, in annual averaged UV–B exposure and the number of days per year with high UV–B, that were strongest in Central America. However, most of the declining amphibian species at Monteverde are forest–floor dwellers that have limited exposure to sunlight. According to Pounds & Crump (1994: p 73), *B. periglenes*, "…normally hide in retreats about 95% of the time, emerging to breed beneath the forest canopy, typically under heavy cloud cover." Middleton et al. (2001) were unable to describe a plausible mechanism for how increasing UV–B could affect such species. The trends of increasing UV–B may be a by–product of decreased cloudiness (Still et al., 1999) and not related to the amphibian declines that have been observed to date.

Kiesecker et al. (2001) described a mechanism by which climate change and UV–B radiation could directly affect the abundance of *B. boreas* in the Pacific Northwest. ENSO events result in low winter precipitation in the Cascade Mountains, and in the following spring, toad embryos develop in shallower water than in years with high winter precipitation. Kiesecker et al. found a significant regression between depth at which embryos develop and mortality. At depths less than 20 cm, infection by the pathogenic water mold *Saprolegnia ferax* was greater than 50%. Kiesecker & Blaustein (1995) demonstrated experimentally that *B. boreas* embryos were susceptible to *S. ferax* only in the presence of UV–B radiation. Kiesecker et al. (2001) exposed *B. boreas* embryos to ambient sunlight and sunlight with UV–B removed by mylar filters at 3 depths (10, 50, and 100 cm). Mortality of embryos exposed to ambient sunlight exceeded mortality of embryos protected from UV–B only in the shallowest treatment. Kiesecker et al. (2001) concluded that in ENSO years, embryos develop in shallower water, are exposed to higher doses of UV–B radiation, and consequently suffer catastrophic mortality from infection by *S. ferax*.

Analyzing global change as an explanation for amphibian declines

Although Pounds et al. (1999) provide correlations between decline of anurans in Costa Rica and ENSO events, the mechanisms causing the declines are still a matter of speculation. The lifting cloud bank hypothesis (Still et al., 1999) is a computer simulation, and temperature data collected by Pounds et al. (1999) are not consistent with its predictions. Pounds et al. recorded a decrease in the difference between daytime and nighttime temperatures, but clear skies should result in lower nighttime temperatures and an increase in the difference. Pounds et al. did record greater frequency of dry season days without precipitation from mist during ENSO years, so it may be that precipitation is much more important that temperature as a factor in the declines of amphibians in the Monteverde region. However, Alexander & Eischeid (2001) point out that the ENSO event in 1982–1983 was stronger than the 1986–1987 event, but it was not coincident with amphibian declines at Monteverde.

The study of *B. boreas* by Kiesecker et al. (2001) shifted one of the emphases in the study of causes of amphibian declines from direct effects of increasing UV–B radiation (Blaustein et al., 1998) to more complex interactions (Blaustein & Kiesecker, 2002). Pounds (2001) stated that Kiesecker et al. (2001), "…identify a complete chain of events whereby climate change causes wholesale mortality in an amphibian population." However, this is a significant overstatement. Kiesecker et al. (2001) linked climate change, UV–B radiation, and disease with excessive mortality of embryos. It has not been demonstrated that this has affected the abundance of adult toads. Kiesecker et al. (2001) stated, "*If* bouts of high embryo mortality occur with greater regularity and intensity, they *may* result in population declines." However, the populations of toads studied by Kiesecker et al. have not declined (Olson, 2001), and sensitivity analysis suggests that abundance is not strongly related to changes in embryo mortality (Biek et al., 2002; Vonesh & De la Cruz, 2002). Furthermore, the mechanism of embryo mortality

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proposed by Kiesecker et al. (2001) is open to question. In the mountains of the western U.S., amphibian breeding phenology is controlled by snowmelt, and low winter precipitation results in earlier breeding (Corn & Muths, 2002; Corn, 2003). Earlier breeding reduces exposure of embryos to UV–B (Merilä et al., 2000; Corn & Muths, 2002). Lost Lake, the primary study site of Kiesecker et al. (2001) is among the most transparent to UV–B of any amphibian breeding site in the Cascades (Palen et al., 2002). Therefore, it may not be appropriate to generalize based on results of studies at this site.

Population declines associated with infection by the pathogenic fungus *Batrachochytrium dendrobatidis* have been documented in amphibians in many regions, including Spain (Bosch et al., 2001), and Daszak et al. (2003) consider chytridiomycosis to be an emerging infectious disease (EID). An EID may be caused by a common pathogen that increases in range and virulence following an environmental change (Daszak et al., 2001), and because *B. dendrobatidis* suvives best at moderate temperatures (23° C) and dies at 30° C (Longcore et al., 1999), it is tempting to hypothesize that climate change may be playing a role in chytridiomycosis as an EID. There have been several attempts to relate amphibian declines, some of which may be caused by chytridiomycosis, to recent weather patterns and climate data, none of which have been very successful. Numerous species of rainforest frogs have disappeared or declined in eastern Australia, primarily in the mountains of eastern Queensland and northeastern New South Wales (Laurance et al., 1996; Mahony, 1996). Laurance (1996) analyzed weather data, and although wet season rainfall was reduced in the 5 years preceding declines, he concluded this was not out of the range of normal variation and was insufficient to have caused the declines.

Alexander & Eischeid (2001) examined climate data for regions with documented amphibian declines (Colorado, Puerto Rico, Central America, and Queensland), and found results similar to Laurance (1996). There were few similarities in weather among areas before the declines occurred, and although warmer temperatures occurred during the onset of declines in Puerto Rico and Queensland, these were not extreme. Alexander and Eischeid concluded that abnormal temperature and precipitation were unlikely to have caused the declines directly. Because the chytrid fungus may survive better at cooler temperatures, and is likely to be transmitted among amphibians by a motile aquatic stage, warmer and drier climate trends seem unlikely to promote outbreaks of chytridiomycosis. However, we need considerably more information before rejecting a link between climate change and disease.

Davidson et al. (2001, 2002) examined the geographic patterns of the declines of several amphibian species in California, related to climate, UV–B radiation, urbanization, and agriculture. They hypothesized that climate change would be manifested in declines related to related to latitude, elevation, and precipitation. Specific predictions were more declines at lower latitudes and elevations and at drier sites. However, they found no evidence to support this hypothesis. Declines of several species occurred downwind of agricultural areas, suggesting that airborne contaminants might be the greatest threat.

Future effects of climate change on amphibians

The relationship between current amphibian declines and climate change may be ambiguous, but it is fairly easy to predict serious consequences to amphibian abundance and distribution if predictions of climate change during the next century come to pass. MacCracken et al. (2001) and Hulme & Viner (1998) describe potential outcomes for the United States and the tropics, respectively. MacCracken et al. (2001) describe outcomes of climate models based on increasing atmospheric CO_2 concentrations. Global mean temperatures would rise 1.2–3.5°C, but increases would be higher at mid to high latitudes and greater over continents than over oceans. Warming over the U.S. would be between 2.8 and 5°C and result from higher winter and nighttime temperatures. Global precipitation will increase, but predicting local patterns is difficult. Less snow is expected, reducing the area of snow cover during winter. Higher summer temperatures will increase evaporation, reducing soil moisture. Extreme precipitation events will become more frequent. In the tropics, the predictions described by Hulme & Viner (1998) are qualitatively similar: increased temperature, increased length of the dry season, decreased soil moisture, and greater interannual variation in rainfall.

Donnelly & Crump (1998) predict that tropical amphibians will suffer reduced reproductive success, reduced food supply, and a disruption in breeding behavior and periodicity. They predict that the effects will be greatest on endemic species, those species restricted to a specific location and which usually have specialized ecological requirements. Donnelly and Crump note that if all the endemic amphibians were lost in three Central American countries, Costa Rica, Panama, and Honduras, amphibian diversity in those countries would decrease by 17 to 26%. Thomas et al. (2004) forecast similar changes in a suite of tropical anurans in Australia by the year 2050, based on shrinkage of available habitat resulting from predicted changes in temperature and precipitation. Teixeira & Arntzen (2002) used a similar approach to predict reduced distribution of the Golden–striped Salamander, *Chioglossa lusitanica*, in Spain and Portugal between 2050 and 2080.

Thomas et al. (2004) predicted the smallest risk of extinction for species inhabiting boreal and alpine habitats. However, several species of amphibians in the mountains of the western U.S. have

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declined in the past 20–30 years (Corn, 2000), and climate models predict that rising winter temperatures will dramatically reduce the extent and duration of mountain snow packs in most of this region in the next 50–100 years (McCabe & Wolock, 1999; Leung et al., 2004; Stewart et al., 2004). If true, this will result in earlier breeding by most montane amphibians (Corn & Muths, 2002; Corn, 2003), increasing the strain on populations that may already be in decline. The consequences of earlier breeding may include more frequent exposure to killing frosts (Inouye et al., 2001). The duration of the larval period may increase, because water temperatures warm more slowly in early spring. Amphibians breeding in lentic water typically have high larval mortality, and there is strong selection for reducing the time spent as larvae (Berven, 1982). Reduced water storage as snow, earlier runoff, and an increase in evaporation due to warmer summer temperatures will likely reduce the hydroperiod of temporary ponds, but specific predictions are complex and require linking hydrologic models to climate change predictions. Any significant change in occurrence or hydroperiod of temporary ponds could have serious effects on amphibian diversity. Several amphibian species use temporary ponds as their primary breeding habitat. Predators and competition from other amphibians restricts the ability of these species to switch to more permanent water (Wellborn et al., 1996; Snodgrass et al., 2000). Threats to montane amphibians may be more severe than predicted generally for boreal and alpine species by Thomas et al. (2004).

Finally, an increase in the frequency of severe weather events is likely to cause problems for amphibians. Drought has been documented several times as a serious challenge to population persistence (Corn & Fogleman, 1984; Weygoldt, 1989; Kagarise Sherman & Morton, 1993; Pounds & Crump, 1994; Stewart, 1995; Osborne et al., 1996). Other extreme events, such as floods, frosts, and hurricanes, have been implicated as causes of declines at regional scales (Heyer et al., 1988; Woolbright, 1997; Corn, 2000). Increases in catastrophic mortality are difficult for stable populations to cope with, but for those amphibian species already in decline, increases in severe weather events could make survival extremely difficult.

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