
Climate Variability in Regions of Amphibian Declines

MICHAEL A. ALEXANDER* AND JON K. EISCHEID

Climate Diagnostics Center, National Oceanic and Atmospheric Administration-Cooperative Institute for Research in Environmental Sciences, Mail Code R/CDC1, 325 Broadway, Boulder, CO 80305-3328, U.S.A.

Abstract: We explored the relationship between amphibian declines and climate variations in Colorado (U.S.A.), Puerto Rico, Costa Rica-Panama, and Queensland (Australia) through two sources of data: output from the National Center for Environmental Prediction "reanalysis system" and area-averaged station data. The reanalysis system merges observations from airplanes, land stations, satellites, ships, and weather balloons with output from a weather-forecast model to create global fields of atmospheric variables. Station data consisted of temperature and precipitation measured with thermometers and rain gauges at fixed locations. Temperatures were near normal in Colorado when the amphibian declines occurred in the 1970s, whereas in Central America temperatures were warmer than normal, especially during the dry season. The station data from Puerto Rico and Australia indicated that temperatures were above normal during the period of amphibian declines, but reanalysis did not show such a clear temperature signal. Although declines occurred while the temperature and precipitation anomalies in some of the regions were large and of extended duration, the anomalies were not beyond the range of normal variability. Thus, unusual climate, as measured by regional estimates of temperature and precipitation, is unlikely to be the direct cause of amphibian declines, but it may have indirectly contributed to them. Previous researchers have noted that the declines appear to have propagated from northwest to southeast from Costa Rica to Panama and from southeast to northwest in Queensland, Australia. Wind has the potential to transport pathogens that cause amphibian mortality. The mean direction of the near-surface winds tended to parallel the path of amphibian declines from July-October in Central America and from May-July in Australia. The wind direction was highly variable, however, and the propagation rate of amphibian declines was much slower than the mean wind speed. In addition, the most likely pathogen is a chytrid fungus that does not produce desiccation-resistant spores. Thus, if wind is involved in the propagation of amphibian declines, it is through a complex set of processes.

Variabilidad Climática en Regiones de Declinaciones de Anfibios

Resumen: Exploramos la relación entre las declinaciones de anfibios y las variaciones climáticas en Colorado, E.U.A., Puerto Rico, Costa Rica/Panamá y Queensland, Australia por medio de dos fuentes de información: resultados "sistema de reanálisis" del Centro Nacional de Predicción Ambiental y datos de estaciones área-promedio. El sistema de reanálisis combina observaciones de aeroplanos, estaciones terrestres, satélites, barcos y globos climatológicos, con resultados de un modelo de predicción climatológica para crear campos globales de variables atmosféricas. Los datos de estaciones fueron de temperatura y precipitación medidos con termómetros y pluviómetros en localidades fijas. Las temperaturas fueron casi normales en Colorado cuando ocurrieron las declinaciones en la década de 1970, mientras que las temperaturas en Centro América fueron mayores a lo normal, especialmente durante la época de sequía. Los datos de estaciones en Puerto Rico y Australia indicaron que la temperatura fue mayor a la normal durante el período de declinación de anfibios, pero un nuevo análisis no mostró una señal de temperatura tan clara. Aunque las declinaciones ocurrieron mientras las anomalías de temperatura y precipitación fueron grandes y de duración prolongada en algunas de las regiones, las anomalías no rebasaron el rango de variabilidad normal. Por lo tanto, es poco probable que el clima inusual, medido por estimaciones regionales de temperatura y precipitación, sea la causa directa de las declinaciones de anfibios, pero pudo haber contribuido indirectamente a ellas. Investigaciones previas notan que las declinaciones parecen haberse propagado de noroeste a sureste de

*email maa@cdc.noaa.gov

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Costa Rica a Panamá y de sureste a noreste en Queensland, Australia. El viento tiene el potencial de transportar patógenos que causan mortalidad de anfibios. La dirección promedio de los vientos superficiales tendió a ser paralela al camino de las declinaciones de anfibios de julio a octubre en Centro América y de mayo a julio en Australia. Sin embargo, la dirección del viento fue altamente variable y la tasa de propagación de declinaciones de anfibios fue mucho más lenta que la velocidad promedio del viento. Adicionalmente, el patógeno más probable es un hongo quitrido que no produce esporas resistentes a la desecación. Por tanto, si el viento está implicado en la propagación de declinaciones de anfibios, lo es por medio de un complejo conjunto de procesos.

Introduction

Over the past 25 years, many amphibian populations have been diminished greatly or have disappeared entirely (Carey 2000). Since the early 1970s, population declines have occurred in North and South America, Puerto Rico, and Australia (Carey et al. 2001, this issue). In some locations, clear explanations exist for amphibian declines, such as habitat destruction or introduction of exotic species. The reasons for many of the amphibian declines are not clear, however, although they share common attributes: frogs and toads that live in high-elevation streams appear to be the most affected. It has recently been proposed that a chytridiomycete fungus (*Batrachochytrium*) has been the proximate cause of death for many of these species (Berger et al. 1998; Berger & Speare 1999; Pessier et al. 1999; Carey 2000). Even if this hypothesis is confirmed, many questions remain. Have environmental factors such as climate change or pollution stressed the amphibians and made them more susceptible to disease? Could these factors alter the virulence of the pathogen? Is the fungus being transported to new regions where the amphibians have not been exposed previously? We explored the possibility that variation in climate was correlated with amphibian declines at specific locations.

The influence of climate variability on the range and behavior of organisms has received a great deal of attention in the recent literature. Periodic warming of sea-surface temperatures in the tropical Pacific associated with El Niño affects organisms around the globe (Glynn 1990), including the land and ocean ecosystems in the eastern equatorial Pacific (Barber & Chavez 1983; Gibbs & Grant 1987), the geographic range of fish (Mysak 1986), and the spread of disease (Nicholls 1993). Changes in the North Pacific ocean-atmosphere system influence phytoplankton productivity (Venrick et al. 1987; Polovina et al. 1995) and salmon catch (Mantua et al. 1997). Warming caused by an increase in carbon dioxide is likely to affect ecosystems (Intergovernmental Panel on Climate Change 1996), including the range, abundance, and breeding cycles of many species (Beebee 1995; Parmesan 1996).

Several studies have sought to link extremes in weather or climate to amphibian declines. Corn and Fogelman (1984) hypothesized that drought conditions

contributed to the decline of the boreal toad (*Bufo boreas*) in the Rocky Mountains, and Fellers and Drost (1993) proposed dry conditions as the cause of leopard frog (*Rana cascade*) declines in the Sierra Nevada Mountains. Heyer et al. (1988) suggested that a severe frost caused the decline and local extinctions of many frogs in southeastern Brazil in 1979, whereas Weygoldt (1989) proposed that several extremely dry winters during the 1980s were the most likely cause of frog declines in this region. Osborne (1989) attributed the decline of the corroboree frog (*Pseudophryne corroboree*) in New South Wales, Australia, to frequent summer droughts between 1979 and 1984, and Ingram (1990) attributed the disappearance of the southern gastric brooding frog (*Rheobatrachus vitellinus*) and the southern dayfrog (*Taudactylus diurnus*) in southeast Queensland to excessive rainfall in cooler months.

Pounds and Crump (1994) and Pounds et al. (1999) have proposed that the extinction of several species of frogs and toads and changes in the bird and reptile communities at Monteverde, Costa Rica, are related to changes in the climate system. Pounds and Crump found that below-normal rainfall occurred for four seasons in a row, a unique event in the 20-year record, just prior the collapse of the golden toad (*Bufo periglens*) and harlequin frog (*Atelopus varius*) populations in 1987. The warm and dry conditions at Monteverde were attributed to changes in regional climate associated with the 1986–1987 El Niño event. Pounds et al. note that the 1986–1987 El Niño event was part of an upward trend of sea-surface temperatures in the eastern tropical Pacific. They proposed that warm temperatures in the ocean and atmosphere alter the vertical profile of relative humidity in the tropics, including Central America. As a result, air parcels rise to a higher level before reaching saturation, lifting the cloud base and reducing the amount of dry-season mist in the mountains of Costa Rica. Pounds and Crump have suggested several ways in which a reduction of days with mist in the dry season may adversely affect amphibians. For example, a reduction in mist may cause amphibians to gather in large groups, making them more susceptible to parasites or to cloud-borne toxins that might be more concentrated when mist is less frequent. It is not clear, however, why the negative effects on amphibians did not occur during the 1982–1983 El Niño event, when the sea-surface temperatures

in the eastern tropical Pacific Ocean were substantially warmer than during the 1986–1987 event.

Perhaps the most extensive study to date of the relationship between amphibian declines and climate fluctuations was conducted by Laurance (1996). He examined temperature and precipitation records in south, central, and north Queensland which included the period when amphibian populations declined. In general, there was less rain, especially during the wet season, and temperatures were above normal, especially in summer, during the 5 years prior to the frog declines. Although less rainfall and warmer temperatures lead to an increase in drought conditions, Laurance concluded that the moderate departures of temperature and rainfall from their long-term averages were not unique over the 50- to 100-year instrument record. Thus, unusual weather was unlikely to have been the primary cause of the frog extinctions. Nicholls (1984) indicated that the onset of the wet and dry seasons is highly variable in northeast Australia. By using fixed periods to define the seasons, Laurance may have underestimated the rainfall in the wet season, overestimated it in the dry season, and missed some precipitation extremes (R. Alford, personal communication).

We expanded on the analyses in these previous studies by using two data sources to evaluate whether climate variability was a direct or indirect factor in amphibian declines. We limited our analyses to die-offs of frog and toad species (order Anura); other amphibians, including salamanders and caecilians, were not considered. We explored the relationship between climate and amphibian declines in four regions: Colorado (U.S.A.) Puerto Rico, Costa Rica–Panama, and Queensland (Australia). These regions were chosen because they contain fairly long and reliable weather records and because the location and times when amphibians disappeared are fairly well documented for these places. The period when the amphibian populations decreased varies from site to site within a given region (Table 1). In Colorado, the first major population crash of the boreal toad (*Bufo boreas*) was observed in 1974 (Carey 1993), although a few dead toads were noted in 1973 (C. Carey, personal communication). A second set of declines occurred in the late 1990s in the mountains of northern Colorado (several dead animals were found in Rocky Mountain National Park in 1996), followed by a more pronounced reduction in toad populations at several locations in 1999 (C. Carey, personal communication). Although extinctions of local amphibian populations have been observed in Central America over the past 15 years, many species declined in 1993–1994. Prior to 1998 there were three widely separated areas of decline along the east coast of Australia. We focused on northeast Queensland, where many local populations have become extinct since 1990.

Given the sensitivity of anurans to heat and moisture (Rome et al. 1992; Shoemaker et al. 1992), we examined

time series of temperature and precipitation data, including the magnitude and duration of anomalies in these variables during the periods when the anurans declined. The declines also appear to have propagated from northwest to southeast in Central America (Lips 1999) and from southeast to northwest in Australia (Laurance 1996). In these two regions, we examined whether or not the apparent path of the declines is consistent with the mean wind direction and changes in the meridional (north-south) component of the wind. Wind may assist in the transport of pathogens or hosts for the pathogens, such as insects. Wind could also transport anthropogenic substances, such as pesticides, that might kill amphibians outright or make them more susceptible to disease.

Methods and Data Sets

Our main analysis method consisted of examining extended time series (>50 years) of precipitation and near-surface air temperature and wind data, so that the conditions during amphibian declines could be compared to periods before and after the declines occurred. Although historical observations of amphibian population size do not exist in many locations, it is generally believed that the number and extent of extinctions and rapid declines over the past 30 years is very unusual. Thus, examining extended climate records is useful because climate anomalies from 1900–1970 probably did not decimate amphibian populations.

We also considered comparing climate variability in the regions where amphibian die-offs occurred to climate conditions in regions with healthy amphibian populations. As discussed in detail by Carey et al. (2001, this issue), several factors make such comparisons problematic, because differences in elevation, longitude, latitude and anthropogenic changes to the environment can have a large effect on climate and how amphibians respond to climate variability.

Given that the decline in amphibian populations extends over broad areas and that weather stations do not exist in many of these remote locations, we believe that it is useful to use regional climate indices to study anuran declines. There are several potential sources of regional-scale data, including observations collected by conventional methods such as thermometers and rain gauges at weather stations, measurements taken from remote sensors on satellites, and data-assimilation systems that combine various sources of observations with information provided by atmospheric models. There are several benefits to using data-assimilation systems rather than conventional or satellite data. Assimilation systems combine a number of different data sources in a dynamically consistent manner and provide global atmospheric fields on a fixed grid at regular intervals. Assimilation systems are

Table 1. Location and period of amphibian declines.

Region	Center of grid box ^a		No. of stations ^b		Period of decline	Reference
	latitude	longitude	temperature	precipitation		
Central Colorado	30°03'N	106°53'W	45	38	1973-1982 1996-1999	Carey 1993 C. Carey, personal communication
Costa Rica-Panama north (Monteverde) central (Las Tablas) south (Fortuna)	8°34'N	82°30'W	15	40	1986-1988 1993-1994 ^c 1997-1998	Pounds & Crump 1994 Lips 1998 Lips 1999
Puerto Rico	18°05'N	67°50'W	33	74	1982-1992	Joglar & Burrowes 1996
Queensland, Australia southeast (Brisbane) central-east (Eungella) northeast (Townsville- Cooktown)	26°45'S 21°06'S 18°05'S	148°30'E 148°30'E 146°15'E	10	9	1979-1981 1985 1990-1993 ^c	Laurance 1996

^aThe latitude and longitude mark the center of the reanalysis and station grid squares.

^bNumber of ground stations within the 2 × 2.5° square for which temperature and precipitation data were taken.

^cPeriod of study focus.

currently the best source for regional-scale wind data because winds are difficult to measure directly in remote locations. We also used temperature and precipitation data from weather stations in Colorado, Puerto Rico, Central America, and Australia to cross-validate the results obtained from the assimilation system.

Several factors make the direct use of satellite data impractical for our analyses. The maximum duration of research-quality temperature and precipitation data sets obtained from satellites (e.g., Spencer 1993; Reynolds & Smith 1994; Christy et al. 1998; Janowiak & Xie 1999) is currently 15–20 years long. Until recently, precipitation-data satellite sensors yielded large uncertainties in precipitation values based on measurements taken over land and ice (Carleton 1991). In addition, these satellites measured conditions through a thick atmospheric layer. Thus, the remotely sensed temperature could be quite different than the actual near-surface air temperature (Hurrell & Trenberth 1996, 1998). Many of these problems have been greatly reduced with the introduction of new instruments on satellites launched in the last 3 years (e.g., see <http://trmm.gsfc.nasa.gov/>, <http://terra.nasa.gov/>, and <http://pm-esip.msfc.nasa.gov/>). Unfortunately, the introduction of this technology occurred after most of the amphibian declines we wished to study.

The Reanalysis Data-Assimilation System

Weather forecasts based on computer models depend not only on the model equations but also on conditions at the start of the forecast. The weather-forecast models and the procedures used to initialize them have increased in complexity since the first model forecasts were made in the late 1950s. Data-assimilation systems have been developed to access observations from many sources, eliminate data with errors, and then incorporate the

remaining data into forecast models. Beginning in the 1970s it was realized that the blended observational-model output from assimilation systems could be useful for studying climate. Frequent changes in data-assimilation systems needed to improve forecasts, however, introduced spurious transitions into the long-term climate record. For example, estimates of the surface temperature over the tropical Pacific Ocean abruptly increased by about 2° C in 1986 as a result of a change in the assimilation system of the National Center for Environmental Prediction (NCEP). To address this problem, NCEP developed a reanalysis system in which the same global data-assimilation system was used in conjunction with observations collected over the last five decades, creating a consistent database for climate studies.

The NCEP reanalysis system is described in detail by Kalnay et al. (1996). Reanalysis output, including the data used in our analyses, is available at <http://www.cdc.noaa.gov/cdc/reanalysis/reanalysis.shtml/>. Originally, reanalysis output covered the period 1958–1998, but it has since been extended from 1948 through the present. We studied the period 1948–1999. The reanalysis system includes an atmospheric general-circulation model and observations of sea-surface temperature, sea ice, snow cover, and soil wetness that serve as boundary conditions for the model (land temperatures are simulated by the model); observations of atmospheric quantities from many different types of instruments; quality control procedures for eliminating or reducing data errors; and a statistical method that blends the observations with the model-generated fields. The output from the reanalysis system includes global fields of temperature, precipitation, clouds, winds, and more than 100 other variables with a horizontal resolution of approximately 210 km² on 28 unequally spaced vertical levels.

Observations obtained from aircraft, buoys, ground

stations, satellites, ships, and weather balloons are incorporated into the reanalysis system at 6-hour intervals. Starting in 1948, aircraft and weather balloons provided measurements of temperature, wind, and humidity throughout the atmosphere, whereas ships, buoys, and land stations provided measurements of temperature, wind, humidity, and pressure at the surface. Satellites supplied observations of temperature over the depth of the atmosphere and the speed and direction of winds based on the movement of clouds. Since the mid-1970s more than a million satellite observations have been incorporated into the assimilation system every 6 hours. Sophisticated statistical procedures that consider relationships among different atmospheric variables and the error characteristics of the different data sources are used to interpolate observations to the model grid.

Output from the reanalysis system has some deficiencies. Some variables, such as precipitation, are not well constrained by observations and depend more on the physics of the model. Currently, global models are only partly successful at simulating clouds and precipitation. Mountains are highly smoothed, and small-scale features such as thunderstorms are not simulated because of the limited model resolution. Finally, the number of observations per day has increased over time, so the atmospheric fields are likely to be more accurate in the later part of the record.

Station Data

Vose et al. (1992) and Peterson and Vose (1997) compiled temperature data recorded in 2-m-high shelters and precipitation data obtained from rain gauges at ground stations around the world to form the Global Historical Climatology Network. The record lengths of the stations within the network vary: some have data as early as 1850, and others end before 1990. Eischeid (1995) performed additional consistency checks on the data in the network and eliminated data from stations with <20 years of observations for the period 1951–1980. The station records have been updated to include observations through 1999. The data within a 2.5° latitude-longitude grid were then averaged together. They consist of monthly temperature and precipitation anomalies, which are departures of individual monthly values from the 1951–1980 mean of that calendar month. The monthly anomalies have been summed to form annual anomalies to emphasize lower-frequency variability, fluctuations that occur over several years or longer. The station data are likely to provide a better estimate of precipitation than the reanalysis system. The station data set has problems as well, including instrument error, differences between how observers read the instruments, changes in station location, variation in the number of reports over time, and the strong influence of local topography on climate.

Comparison of Reanalysis and Station Data

The level of agreement between reanalysis (from here on taken to mean the output from the reanalysis system) and the station data provides a measure of the reliability of climate signals in the regions of amphibian declines. The two data sets are nearly independent of each other, because surface air temperature and precipitation data from stations were not used as input into the reanalysis system. We compared the two data sets by correlating reanalysis with the station estimates of monthly temperature and precipitation anomalies in the four study regions between 1948 and 1999. The correlations between the two data sets for temperature anomalies in Colorado, Costa Rica–Panama, Puerto Rico, and Queensland, Australia, were 0.81, 0.55, 0.53 and 0.80, respectively. The corresponding correlations for precipitation were 0.37, 0.18, 0.52, and 0.67, respectively. As expected, the two estimates of temperature were more highly correlated than precipitation in all four regions because of the highly variable nature of precipitation and the errors in rain and snow values provided by data assimilation systems. The highest correlations for both temperature and precipitation were in Queensland. The correlations were low (<0.5) for precipitation in Colorado and Costa Rica–Panama. Given the large sample size (624 months), all of the correlations were significant at the 99% level. Although the correlations indicate general agreement between the two data sets, differences between them exist, especially for precipitation over Colorado and central America.

Results

Temperature and Precipitation

COLORADO

We examined the temperature and precipitation values from the reanalysis system and station records for central Colorado (Fig. 1). The median temperature and precipitation values for each calendar month over the period 1948–1999 obtained from reanalysis were used to show the typical seasonal cycle. There was a strong seasonal cycle in temperature that ranged from about -10°C in January to 19°C in July. The narrow range between the 13 warmest and coldest months (i.e., the upper and lower quartiles as shown by the dashed lines in Fig. 1) indicates that monthly temperature anomalies were small relative to the mean seasonal cycle. Individual monthly values for 1972–1975, the years during which the declines first occurred in Colorado, indicate that conditions were warmer than normal from February to May in 1972 and that March of that year was the warmest in the 52-year record. Precipitation is more variable relative to the mean seasonal cycle than is temperature: one or two

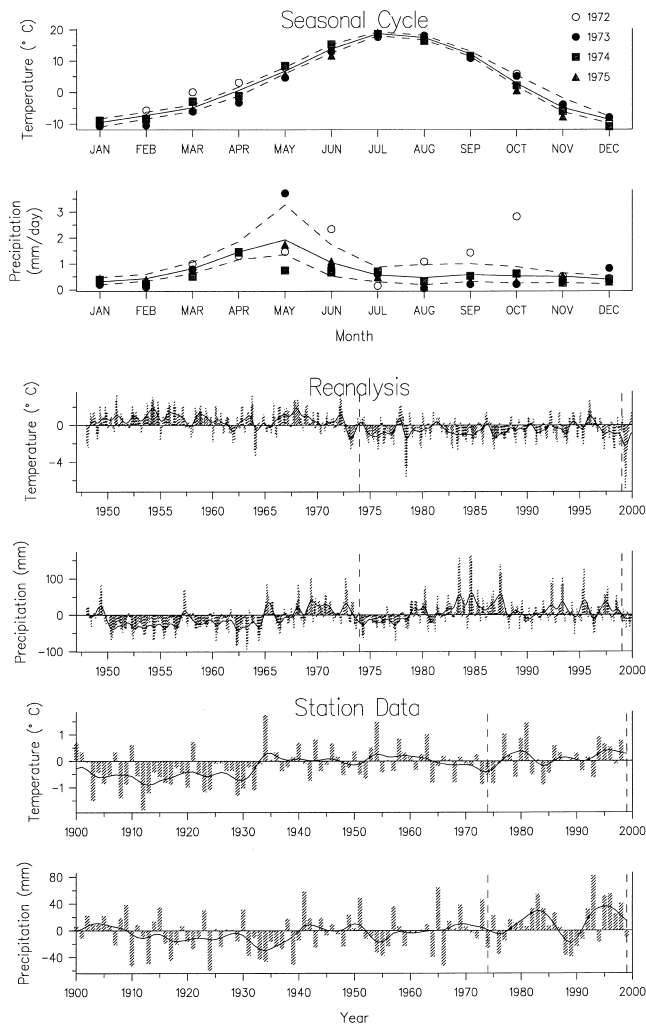


Figure 1. Temperature and precipitation values from reanalysis and station data in central Colorado. The median (solid line) and upper (75%) and lower (25%) quartiles (dashed lines, respectively) for temperature and precipitation from reanalysis during the years 1948–1999 (top two panels). The individual monthly values for the years 1972–1975 are shown in the seasonal cycle graphs. In the reanalysis graphs (middle two panels), vertical lines indicate 3-month averages of temperature and precipitation anomalies, and the solid line is a smoothed version of this reanalysis data based on a 9-point, low-pass filter that emphasizes periods longer than approximately 3 years. The temperature and precipitation anomalies for the station data for the period 1900–1999 are shown in the two station-data graphs (bottom two panels). Station-data anomalies are computed relative to the 1951–1981 period, vertical bars indicate annual anomalies, and the solid line is a filtered version of the data emphasizing periods longer than about 8 years. The dashed vertical lines in reanalysis and station-data graphs denote the approximate time of the major declines in amphibian populations, 1974 and 1999.

strong storms can influence the precipitation total for an entire month. On average, the maximum precipitation of approximately 2.3 mm/day occurs in May, whereas <1 mm/day falls from July through March. Perhaps the most persistent precipitation anomalies during 1972–1975 were the wet conditions in June and August–October of 1972, all of which were in the upper quartile for precipitation.

Monthly temperature and precipitation anomalies for the 52-year reanalysis record and a smoothed time series of these anomalies (Fig. 1) indicate a transition to somewhat cooler and drier conditions during 1973, when the first indications of declines were noted. Temperatures also tended to be below normal during the second period of declines in the late 1990s, especially during 1999. A large negative temperature anomaly of almost 10° C occurred in July of 1978, when many days were below freezing. Although the abnormally cold conditions may have stressed the anurans, this event occurred several years after the rapid declines began in the mountains of central Colorado.

Annual temperature anomalies obtained from an average of station data from central Colorado for the period 1900–1999 (Fig. 1) also indicate that the mid-1970s were relatively cold, but the intensity and duration of the abnormally cold conditions were stronger in the first 30 years of the century than in the 1970s. The station data suggest that precipitation was near normal during the first half of the 1970s.

We examined the climate conditions during the two main periods of amphibian die-offs in central Colorado by comparing the monthly temperature and precipitation anomalies from reanalysis for 1973–1976 and 1996–1999 (Fig 2). For a set of measurements in which the samples are independent and normally distributed, approximately 5% of the values are beyond ± 2 times the standard deviation (dashed lines in Fig. 2). Thus, based on statistical probability, monthly values would exceed these bounds approximately two or three times over a 4-year period ($0.5 \times 48 \text{ months} = 2.4 \text{ months}$). Even if these assumptions are not fully realized, anomalies that exceed twice the standard deviation are large and relatively uncommon. During 1973 and 1996, when the first few dead specimens were found, temperature and precipitation anomalies were generally near normal. Even the large amount of precipitation that fell in May of 1973 did not exceed twice the standard deviation. There also was no clear correspondence between the anomalies in 1973 and 1996. For example, the first half of 1973 was colder than normal (negative anomaly), whereas temperatures were generally above normal during the first 6 months of 1996. Perhaps the most exceptional anomalies in the two periods occurred in the spring of 1999, when extremely cold temperatures may have contributed to the success of the fungus in attacking boreal toads. But there were no correspondingly large negative

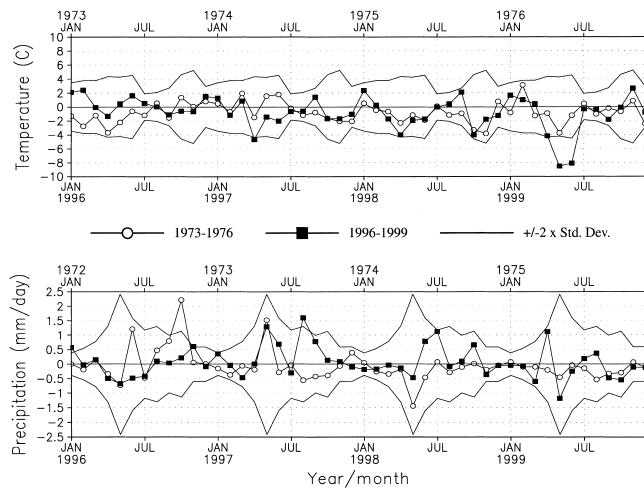


Figure 2. Monthly temperature and precipitation anomalies for central Colorado from reanalysis for the periods 1973–1976 (circles, axis labeled at top) and 1996–1999 (squares, axis labeled on bottom). Dashed lines indicate plus and minus twice the monthly standard deviation, where the values repeat each year. In order to facilitate the comparison between anomalies in 1973 and 1996, the first 4-year period begins 1 year later than in Fig. 1.

temperature anomalies in 1974, when the boreal toad and leopard frog declines began.

COSTA RICA—PANAMA

The seasonal cycle in temperature for the Costa Rica–Panama region has a range of only 1° C, with a maximum of 24.5° C in March (Fig. 3). The first 4 months of the year are substantially drier than May–December (Fig. 3). During 1991–1994, when many die-offs occurred in Costa Rica, conditions were warmer and drier than normal in February and March, the heart of the dry season. Reanalysis indicates that temperatures were above normal in this region of Central America during two of the three main periods of decline, 1986–1987 and 1993–1994. The warm air temperatures over Central America during these years are associated with El Niño events that occurred in the nearby eastern tropical Pacific Ocean. Amphibian declines in Panama began prior to January 1997 (Lips 1999), however, 3 months before the 1997–1998 event began. There also were no reports of anuran population declines during the very strong 1982–1983 El Niño event.

According to reanalysis, Central America was wetter than normal during most of 1986–1987 but drier than normal in the 1990s when the latter two periods of declines occurred (Fig. 3). The station data suggest that the warm temperatures during the 1990s, while above average, were not exceptional. For example, the posi-

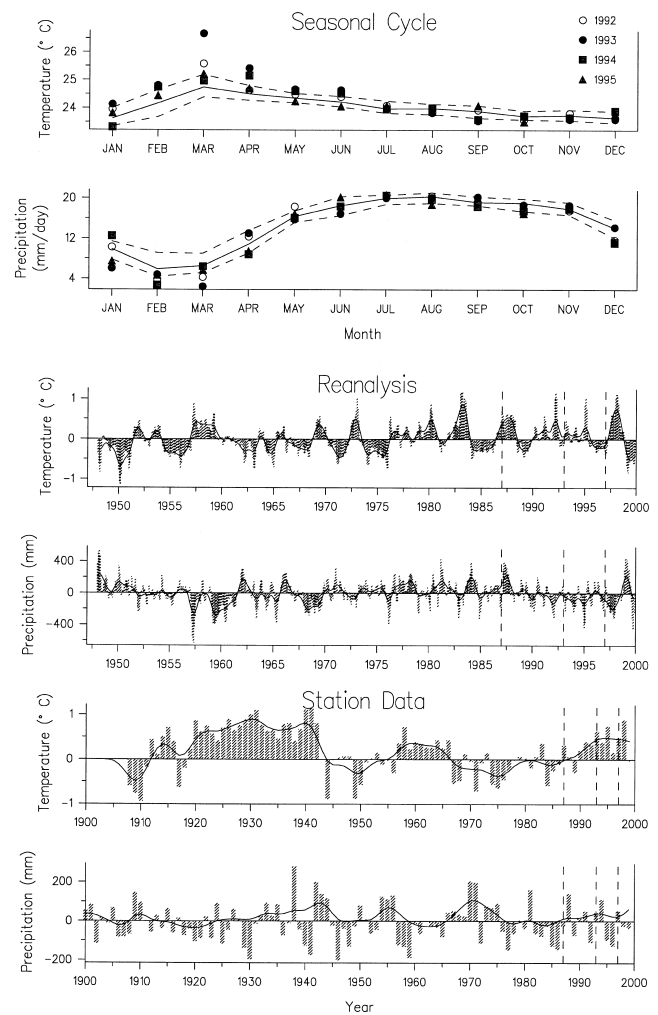


Figure 3. Temperature and precipitation data for the Costa Rica–Panama region displayed as in Fig. 1.

tive temperature anomalies that began around 1920 were much greater in magnitude and duration than anomalies in the 1990s. The precipitation anomalies during the periods of decline also were not exceptional relative to other anomalies in the 100-year rainfall record.

PUERTO RICO

Many of the amphibian declines in Puerto Rico appear to have occurred during the 1980s and early 1990s, although some frog species may have become extinct as early as 1974 (Joglar & Burrowes 1996). The mean seasonal cycle of temperature and precipitation are both fairly small; mean conditions are cooler and drier in January through April than during the remainder of the year (Fig. 4). During the first half of 1989, temperatures were cooler than normal; all 6 months were in the lowest quartile. During this 4-year period conditions were drier than normal between May and July, with the exception of June 1990. For

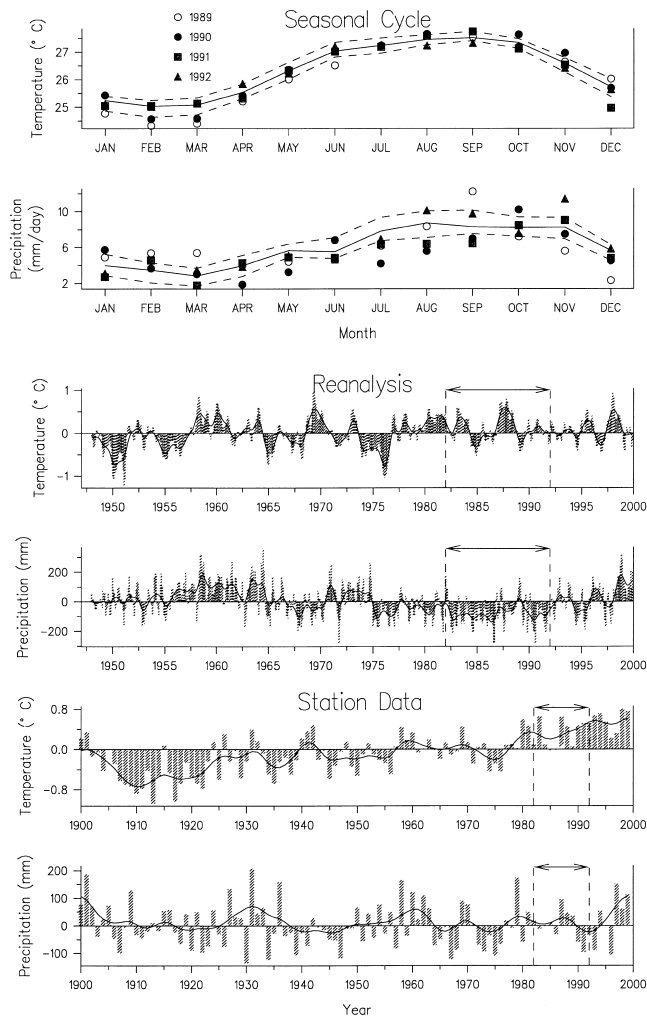


Figure 4. Temperature and precipitation data for Puerto Rico displayed as in Fig. 1. The arrow between the long dashed vertical lines in the reanalysis and station-data graphs indicates that amphibian declines may have occurred over the entire period between 1982 and 1992.

the decade of 1982–1992, when many of the declines are believed to have occurred, the reanalysis temperatures were above normal around 1983 and 1987 (Fig. 4), partly in response to El Niño conditions in the tropical Pacific. Precipitation was below normal for most of the period. Unlike reanalysis, the station data show large positive temperature anomalies from 1982 through 1997. Over the nearly 100-year record, the Puerto Rican station data indicate an upward trend in temperature. Overall, precipitation was below average over the 1980s and early 1990s, except for 1987–1989.

QUEENSLAND, AUSTRALIA

The mean seasonal cycle is moderately strong in northeast Queensland, with temperatures ranging from 25.5° C

in January to 20° C in July (Fig. 5). Precipitation peaks at about 5 mm/day in January–March and drops to <1 mm/day for June–October. The variable nature of the rainfall in this region is illustrated by the precipitation data for the years 1989–1992. In 1990, rainfall was well above normal from March to June, when each month was one of the top three wettest in the 40-year record, but then almost no rain fell from July to November. During 1991, February was the wettest on record, but March through July was relatively dry. Reanalysis indicates a mix of anomalously warm and cold conditions during the period of declines, whereas temperatures from the stations remained above normal beginning around 1980. Both the reanalysis and station data indicate that

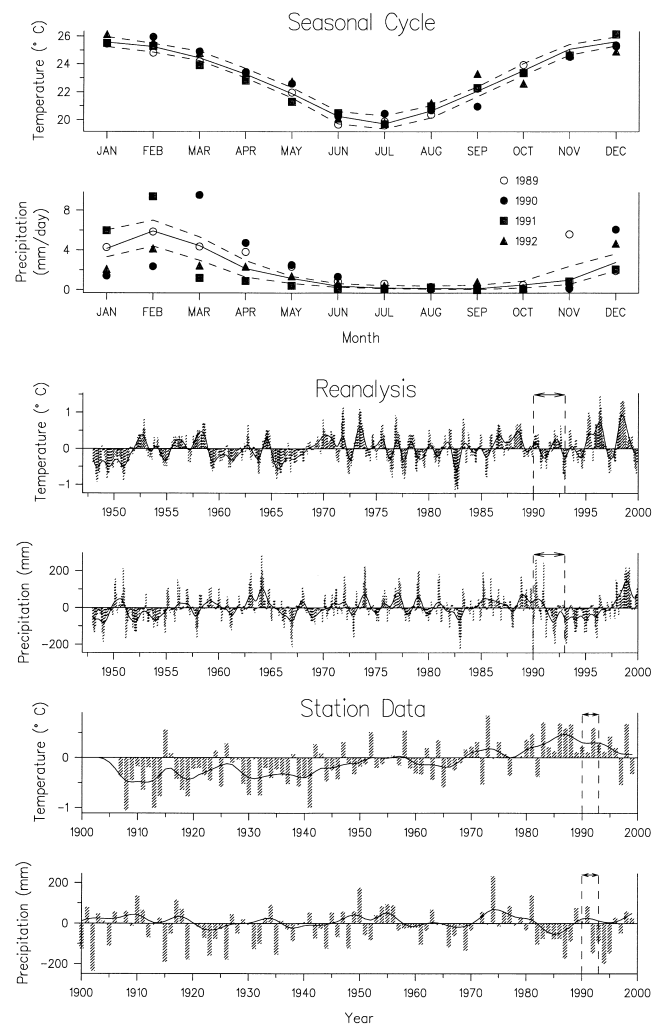


Figure 5. Temperature and precipitation data for northeast Queensland, Australia, displayed as in Fig. 1. The arrow between the long dashed lines in reanalysis and station-data graphs indicates that many species declined or became extinct between 1990 and 1993.

an extended dry period began around 1991, but some of the declines began prior to this time.

Winds

COSTA RICA—PANAMA

The known disappearances and declines of anurans in Central America suggest movement from the northwest to the southeast along the Cordillera de Talamanca range from Monteverde, Costa Rica, in 1987 to Fortuna, Panama, in 1996 (Table 1), which translates to a linear rate of roughly 40 km/year. Using streamlines obtained from the NCEP reanalysis, we examined the relationship between the path of the amphibian declines over Central America and the wind. Streamlines indicate the direction of the wind at a given instant of time. For long-term averages, streamlines tend to coincide with the mean trajectories of individual air parcels. During July–October, the path of frog declines was coincident with the mean wind direction (Fig. 6). During other months of the year, the mean streamlines extend from the northeast to the southwest across Costa Rica and Panama before curving back toward the east over the Pacific Ocean (not shown). In addition, the wind speeds are on the order of 3–5 m/second, three orders of magnitude faster than the observed propagation rate of frog disappearances in Central America. Thus, if atmospheric circulation is involved in the patterns of anuran declines, it is not by the continuous transport of pathogens at the same speed as the mean wind.

We also examined the anomalous meridional (north-south) component of the wind for the Costa Rica–Panama region for all months during 1948–1999. Positive values indicate that the winds were stronger from the south or weaker from the north than normal. From 1985 to 1997, which encompasses the periods of amphibian declines, the anomalies were primarily negative, with maximum values of about 1 m/second (Fig. 6). Thus, the anomalous winds are from north to south, in the direction of anuran declines.

QUEENSLAND, AUSTRALIA

In Australia the declines appear to have moved from southeast to northwest along the coastal mountain regions of eastern Queensland. The first disappearances were noted near Brisbane (south) in 1979, then Eungella (central) in 1985, and the most recent in the Townsville–Cooktown area (north) from 1990 to 1994. Trenerry et al. (1994) also note an apparent northward propagation of declines between Townsville and Cooktown in northern Queensland during the early 1990s. The timing of the amphibian declines in Queensland translates to a linear propagation rate of roughly 120–160 km/year. The long-term mean streamlines for the months of May–July (Fig.

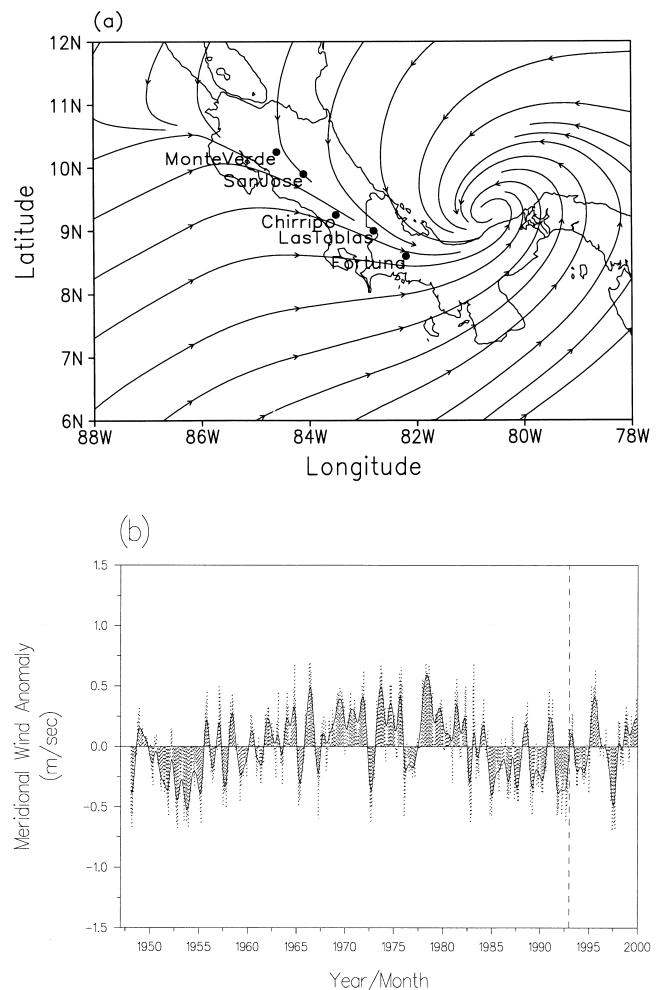


Figure 6. The (a) long-term mean streamlines over Central America for the months July–October based on reanalysis for the period 1948–1999. Streamlines indicate the direction of the wind at any point in the field at a given time. Long-term mean streamlines represent the general path of individual air parcels. (b) Meridional wind anomalies from reanalysis. Vertical dashed line shows 3-month average of anomalies; line is smoothed data that emphasizes periods of >3 years. Negative values indicate that winds are stronger from the north than normal.

7) are parallel to the path of amphibian declines. In other months the flow is more from east to west toward the interior of the continent, especially from September through February. Wind speeds are on the order of 3–5 m/second along the coast but are weaker in the interior and stronger offshore.

The monthly meridional wind-speed anomalies for south, central, and north Queensland (Fig. 7) are fairly well correlated after about 1960. During the period of declines, 1979–1994, both positive and negative anomalies occurred. One may speculate that if the propagation

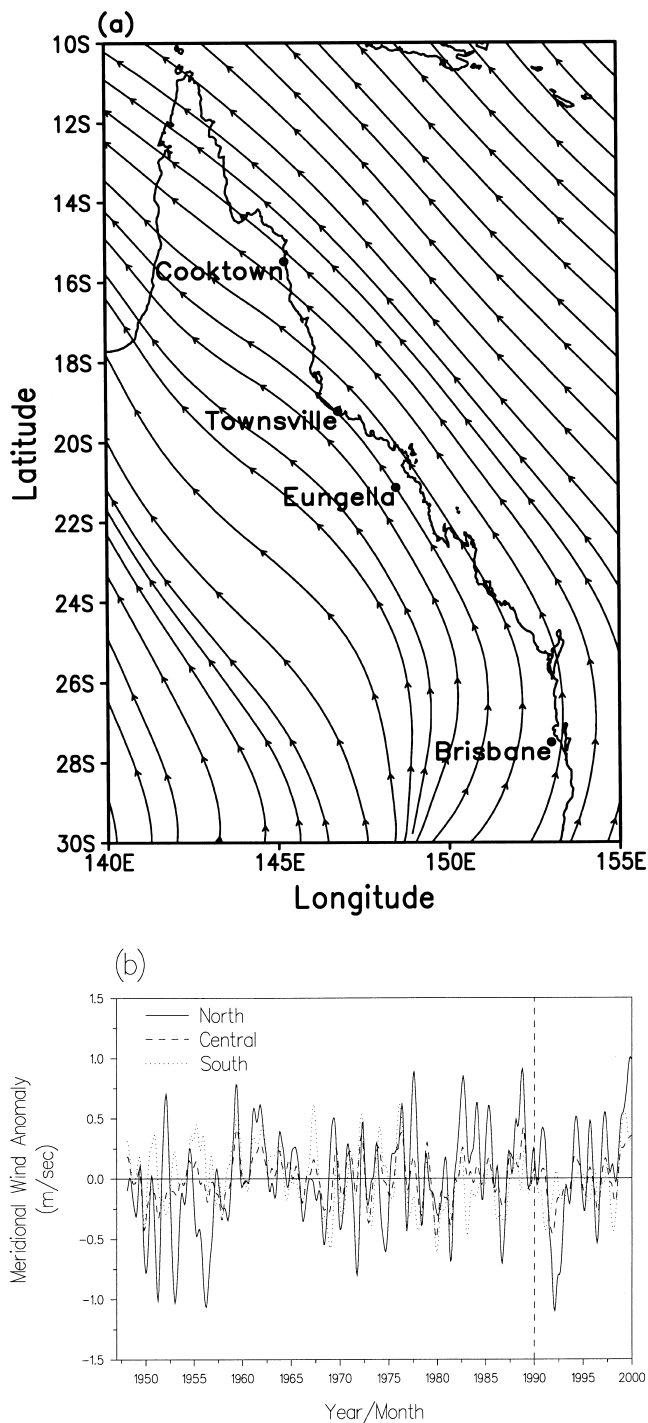


Figure 7. As for Fig. 6, the (a) long-term mean streamlines over eastern Australia for the months May–July from reanalysis. (b) Meridional wind speed anomalies that have been smoothed to emphasize periods longer than about 3 years in south, central, and north Queensland. The location of these three regions are given in Table 1.

was irregular, then the periods of positive anomalies indicative of stronger south-to-north winds in 1982–1985 and 1987–1988 may have contributed to the propagation. We examined the streamlines during these periods, however, and the anomalous winds blew nearly due north rather than along the coast (not shown). Thus, the apparent path of amphibian declines in Queensland does not appear to depend on winds that differed from normal.

Discussion

To study the possible influence of climate variability on amphibians, we employed two distinctly different sources of data: the National Center for Environmental Prediction reanalysis system, which combines a global atmospheric model with many different sources of observations, and station data averaged on a $2 \times 2.5^\circ$ grid. We examined temperature and precipitation in four regions where frog declines and extinctions have been noted, from Costa Rica–Panama in the tropics, to Puerto Rico and northeast Australia in the subtropics, to Central Colorado in midlatitudes.

Reanalysis and the station data were more highly correlated for temperature than for precipitation anomalies, although differences in temperature between the two data sets occurred in some regions during the periods of amphibian decline. Both reanalysis and station data showed that central Colorado exhibited both positive and negative temperature anomalies in the early to mid-1970s. Reanalysis indicated that the Central American region was warmer than normal in the early to mid-1990s, especially during the dry season; and the station data indicated that most years were warmer than normal during this period. Over the 1982–1992 period in Puerto Rico, reanalysis showed a mix of positive and negative temperature anomalies, with warmer than normal temperatures around 1982 and 1987, whereas the station records indicated that temperatures warmed through the 1980s as part of a long-term upward trend. A discrepancy between the data sets also occurred in northeast Queensland. Reanalysis indicated temperature anomalies of both signs in the early 1990s, whereas the station record indicated that 1985–1995 was an exceptionally warm period. The difference between data sets introduces an additional source of uncertainty in attributing frog declines to climate conditions.

In general, conditions were drier than normal in the years during and just prior to the amphibian declines, in agreement with several other studies (Corn & Fogelman 1984; Fellers & Drost 1993; Pounds & Crump 1994; Laurance 1996). It is possible that amphibians experience greater stress during periods of less rainfall, although unusual anuran behavior was not observed prior to the mass mortalities. Both data sets indicate, however, that there

were periods with above-normal precipitation when the amphibians declined. In addition, there was no clear correspondence between anomalous climate conditions in Colorado during the first period of amphibian die-offs in the mid-1970s and the second in the late 1990s.

Some researchers (e.g., Pounds & Crump 1994; Pounds et al. 1999) have sought a link between amphibian declines and atmospheric conditions associated with El Niño and/or carbon dioxide-induced global warming. The climates of Central America and northeastern Australia are strongly influenced by El Niño events (Rogers 1988; Kiladis & Diaz 1989; Nicholls et al. 1996). Measurements and coral cores indicate that El Niño events have been a semi-regular feature of the climate system for at least the past several thousand years, so frogs should be adapted to atmospheric fluctuations associated with El Niño. In addition, the amphibian declines do not appear to coincide with the very strong events that occurred in 1982–1983 and 1997–1998.

Although El Niño events tend to happen about every 2–7 years, there has also been longer-scale variability in sea-surface temperatures in the eastern tropical Pacific. Sea-surface temperatures in this region have shown an upward trend during the twentieth century, with a pronounced tendency for warmer waters starting in 1976 (Nitta & Yamada 1989) and persistently warm ocean temperatures during the early 1990s (Goddard & Graham 1997). Trenberth and Hoar (1996, 1997) and Knutson and Manabe (1998) present evidence that these warm sea-surface temperatures may be associated with an increase in greenhouse gases, although Rajagopalan et al. (1997) and Wunsch (1999) conclude that the recent trend is within normal climate variability. Warming of tropical Pacific Ocean temperatures in addition to that directly due to carbon dioxide and other greenhouse gases may have influenced air temperature, precipitation, cloud height, and other climate variables in Central America, the Caribbean, and northeastern Australia, especially in the 1990s.

Although temperature and precipitation anomalies occurred during the periods of amphibian declines, most, including those in the 1990s, were not exceptional with respect to the rest of the twentieth century. In addition, anurans would have survived numerous climate extremes, such as those associated with ice-ages, over the past thousands of years. It is also not clear why stream-dwelling amphibians would be more susceptible to climate fluctuations than those that breed in ponds and terrestrial species with direct development of eggs. One would expect streams to act as a buffer, making the anurans that live in them less susceptible to climatic extremes. Thus, it is unlikely that recent climate anomalies were the direct cause of the amphibian declines, a conclusion also reached by Laurance (1996) and Laurance et al. (1996, 1997).

It is possible that climate anomalies contributed indirectly to amphibian declines. There are a number of

thermal correlates with historical die-offs of amphibians in the American west that are now thought to be caused by chytridiomycosis. Mass mortalities of amphibians due to chytrid fungus in the western United States appear to have occurred during cold periods (Carey 1993; Taylor et al. 1999; C. Peterson and M. Sredl, personal communications) and require cool temperatures ($<23^{\circ}\text{C}$) for growth in the lab (C. Carey, personal communication). In contrast, many of the declines in Central America, Puerto Rico, and Australia occurred when temperatures were above normal. Perhaps different strains of chytrids with variable thermal optima exist in temperate and tropical environments. The numerous reports of amphibian declines under many different climatic conditions suggest that the temperatures necessary for chytridiomycosis to occur are within the normal range of climate variability. For example, the mountains of the American west are often cold. Indeed, temperatures are normally below 20°C in the central Colorado region studied here (Fig 1).

We also examined the long-term mean wind direction and anomalies in the north-south component of the wind in Central America and along the east coast of Australia, because the declines appear to propagate from northwest to southeast from Costa Rica to Panama and from southeast to northwest in Queensland, Australia. The mean direction of the near-surface winds tends to parallel the path of amphibian declines from July to October in Central America and from May to July in Australia. The anomalous winds were from north to south in Central America but were of mixed sign and amplitude along the coast of Australia during the periods of decline. From a climate perspective, the coincidence of the mean wind direction and the path of the amphibian declines indicates that the mean winds could have assisted in the transport of a pathogen, such as the chytrid fungus. But *Batrachochytrium* appears to be a waterborne pathogen and does not produce spores resistant to desiccation (Berger et al. 1999). Thus, direct transport of the pathogen by the wind seems unlikely. The wind also could carry hosts for the pathogens or toxic substances that make amphibians more susceptible to infection, but there is no evidence that toxins are involved in amphibian declines. In addition, the wind is highly variable and does not blow along the path of declines during many months of the year, and the apparent propagation rate of the amphibian declines is much slower than the mean wind speed. So, if wind is involved in the waves of amphibian declines, it is likely to be part of a complex process.

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