
Amphibian Declines and Environmental Change: Use of Remote-Sensing Data to Identify Environmental Correlates

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Abstract: *Populations of many amphibian species are declining worldwide, and a few species appear to have become extinct. In an attempt to evaluate the potential usefulness of remote-sensing techniques as a tool for identifying the causes of these declines, we compiled a database that contains descriptions of 120 localities, both at which declines have been documented and at which no declines are yet known. The number of species involved, dates and degree of declines, habitat characteristics, and other factors are provided for each locality. Four relatively undisturbed areas in northeastern Australia, Costa Rica-Panama, central Colorado, and Puerto Rico were chosen for examination of environmental correlates coincident with mass mortalities at these localities. We used data predicted by models or collected by satellites, airplanes, or direct sampling on the ground to evaluate variations over time in temperature, precipitation, wind direction, UV-B radiation, and concentrations of certain contaminants at these sites. We asked whether unusual changes in these environmental variables occurred either just in advance of or concurrent with dates of amphibian mass mortalities. The variation in certain environmental variables documented by others (Alexander & Eischeid 2001; Middleton et al. 2001; Stallard 2001 [all this issue]) appears unlikely to have directly caused amphibian deaths. But correlations between these environmental changes and the occurrence of amphibian die-offs invite further investigation into synergistic interactions among environmental variables and possible indirect causal relationships.*

Declinaciones de Anfibios y Cambio Ambiental: Uso de Datos de Percepción Remota para Identificar Correlaciones Ambientales

Resumen: *Das poblaciones de muchas especies de anfibios están declinando en todo el mundo y aparentemente algunas especies se han extinguido. En un intento para evaluar la utilidad potencial de las técnicas de percepción remota como una herramienta para identificar las causas de esas declinaciones, recopilamos una*

base de datos que contine la descripción de 120 localidades en las que se han documentado declinaciones, así como en las que aún no se conocen declinaciones. Para cada localidad se proporciona el número de especies involucradas, las fechas y el nivel de declinación, las características del hábitat y otros factores. Se eligieron cuatro áreas relativamente no perturbadas en el noreste de Australia, Costa Rica/Panamá, Colorado central y Puerto Rico para examinar las correlaciones ambientales coincidentes con la mortalidad en masa en esas localidades. Utilizamos datos predichos por modelos u obtenidos por satélites, aeroplanos o muestreo directo para evaluar las variaciones de la temperatura, precipitación, dirección del viento, radiación ultravioleta-B en el tiempo, y las concentraciones de ciertos contaminantes en esos sitios. Nos preguntamos si ocurrieron cambios inusuales en esas variables ambientales justo antes de o concurrentes con las fechas de las mortalidades masivas de anfibios. La variación en ciertas variables ambientales documentadas por otros autores (Alexander & Eischeid 2001; Middleton et al. 2001; Stallard 2001, todos en este número) no parece ser la causa directa de la muerte de los anfibios. Sin embargo, las correlaciones entre estos cambios ambientales y la ocurrencia de la mortalidad de anfibios requieren de más investigación de las interacciones sinérgicas entre las variables ambientales y las posibles relaciones causales indirectas.

Introduction

Although many possible causes for global amphibian declines have been proposed (Phillips 1990), few studies have provided convincing proof of causal relationships or have attempted to distinguish direct causes (the actual cause of the death of a given population) from indirect ones (sublethal factors that facilitate or promote the effect of the direct factor). Anthropogenic alterations in the environment—habitat destruction, introduction of predators, direct application of pesticides, herbicides, and industrial chemicals—are generally accepted as proximate causes of some amphibian declines (reviewed by Alford & Richards 1999). The causes of mortality in such cases are fairly obvious: for example, clear-cutting of forests or drainage of wetlands modifies the thermal and hydric conditions beyond the tolerance limits of amphibians, their young, and/or their insect prey (Ash 1997).

In other cases, the direct and indirect causes of amphibian declines are less obvious. A surprising number of mass mortalities have occurred in relatively undisturbed areas, such as national parks and wilderness areas of the western United States (Corn & Fogleman 1984; Bradford 1991; Carey 1993; Kagarise Sherman & Morton 1993; Drost & Fellers 1996) and montane rainforests of Central America and Australia (Richards et al. 1993; Pounds & Crump 1994; Laurance et al. 1996; Lips 1998, 1999; McDonald & Alford 1999). Most of these fit the following pattern: die-offs occur over geographically widespread areas; populations experience 50–100% mortality; declines are more pronounced at relatively high elevations or in cold climates; some, but not all, of the total number of amphibian species in a locality experience population declines; mortality occurs principally among metamorphosed individuals; and infectious disease is currently thought to be the direct cause of death (Scott 1993; Berger et al. 1998; Berger et al. 1999; Carey et al. 1999; Daszak et al. 1999).

Although Koch's postulates have not been fulfilled in

most instances to identify positively the causative pathogens, a growing body of evidence implicates the involvement of a skin infection caused by a nonhyphal, parasitic chytrid fungus *Batrachochytrium dendrobatidis* (Chytridiomycota; Chytridiales) in many mass mortalities in Australia, Costa Rica–Panama, and the western United States (Berger et al. 1998, 1999; Carey et al. 1999; Longcore et al. 1999; Pessier et al. 1999). As yet, little is understood about where this fungus originated or how it overwhelms or circumvents the immune defenses of amphibians. The biology of this fungus explains several aspects of the patterns of the dieoffs mentioned above: (1) metamorphosed individuals are stricken primarily because the fungus attacks keratin, a compound that eggs and larvae (except for mouthparts) do not have (Berger et al. 1998; Longcore et al. 1999) and (2) not all species in a given habitat succumb because the fungus is aquatic and cannot infect arboreal or strictly terrestrial amphibians.

Some workers believe that environmental factors are not involved in the emergence of this pathogen or its success in killing amphibians (Daszak et al. 1999), but a number of recent studies documenting the emergence of some, but not all, new pathogens of humans and wildlife have implicated environmental changes as potential indirect causes (Nicholls 1993; de Swart et al. 1994; Herbst & Klein 1995; Lahvis et al. 1995; Colwell 1996; World Health Organization 1996; Colwell & Patz 1998; Hayes & Goreau 1998; Harvell et al. 1999). Climatic factors have also been linked to outbreaks of arboviral diseases of humans (Maelzer et al. 1999). Because of the importance of understanding the causes of amphibian declines and how these causes relate to the larger context of human effects on biological systems, the possibility that various environmental variables have directly or indirectly contributed to amphibian mass mortalities merits further examination.

Although chytridiomycosis is an obvious possibility as a direct cause of amphibian declines at our four study sites, we took a broad approach with this study. We addressed

the question of whether changes in one or more environmental variables (temperature, precipitation, wind direction, ultraviolet light, and concentration of atmospheric contaminants) are correlated with amphibian dieoffs at specific times and locations. Our hypothesis was that marked changes in one or more environmental factor(s) must occur either just before or concurrently with a dieoff to be considered a potential cause. We looked for abnormal changes in given environmental parameters on the assumption that normal variation of an environmental parameter is unlikely to be lethal to amphibians. We also looked for steady increases or decreases in environmental parameters over time on the assumption that such changes might surpass the limits of amphibian tolerances or might promote the ability of a pathogen to overcome the immune defenses of amphibians.

If correlations exist between environmental changes and dates of amphibian declines, further examination is warranted to determine how these changes might directly or indirectly cause amphibian declines. Sublethal environmental changes could contribute to amphibian declines in a multitude of ways, including promoting the conversion of a nonpathogenic to a pathogenic microorganism, affecting the susceptibility of amphibians to pathogens (Carey et al. 1999), affecting the food supply, and diminishing the competitive abilities of a species. Because each environmental variable was studied independently of the others in this project, future study is necessary to determine how synergistic interactions of various environmental factors might affect amphibian populations.

To begin this study, we created a database that includes descriptions of a number of sites at which amphibian declines have been documented and a few at which no declines have been observed. Of these sites, we chose three study areas (tropical mountains of northeastern Queensland, Australia, and of Costa Rica–Panama, and the Rocky Mountains of central Colorado, United States) at which the dates of mass mortalities have been documented and one area (the mountains of Puerto Rico) at which the approximate time of decline has been established. Because these sites are in national parks, wilderness areas, and forest reserves, the effects of humans are not an obvious cause of amphibian declines. Chytrid fungal infections have been associated with dieoffs in Australia, Costa Rica–Panama, and Colorado (Berger et al. 1998, 1999; Carey et al. 1999), but the causes of amphibian declines in Puerto Rico have not yet been established.

Use of Remote-Sensing Techniques for Conservation Biology

A wealth of environmental data exist that have been gathered through remote-sensing instruments on satellites or aircraft. Some of these data are available from the National Aeronautics and Space Administration (NASA)

on the internet (<http://daac.gsfc.nasa.gov>). Our project was one of several selected by NASA to investigate the potential application of remotely acquired data to issues in conservation biology. The individuals who initiated this project are biologists who share interests in amphibian declines and who collectively have had little experience in methodologies, techniques, or types of data associated with remote-sensing technologies. The project that subsequently was fostered by NASA allowed us to access environmental data that had not been evaluated previously in the context of amphibian declines and to learn about remote-sensing techniques that are now being used to track outbreaks of human diseases and the environmental changes that foster them (Hay et al. 1996; Linthicum et al. 1999).

In our search for remotely acquired data sets that documented the temporal change of environmental variables at our four study regions, we discovered two qualities that affect the use of remote-sensing data by the conservation biology community: a relatively large geographical area representing a single value and the temporal availability of the data sets.

The disadvantage of the first quality is that the size of the pixel (the “picture element”) is very large compared with the small size of amphibian breeding sites and represents an aggregate signal from all objects within its boundaries, as discussed by Middleton et al. (2001, this issue). The disadvantages of the second quality are that satellite technology is relatively recent (databases do not go back for more than 20–30 years at best), and discontinuities in data collections have occurred. Long-term data sets are advantageous for evaluating the frequency of abnormal events. Changes in platforms, sensor drift, data-processing algorithms, and innovations in instrumentation have led to misinterpretation of trends in various global variables, such as temperature (Hurrell & Trenberth 1998), thereby requiring expert processing and interpretation of the data sets.

Other potential pitfalls await the naive investigator, including (1) knowing how and where to access the most appropriate remotely sensed data; (2) knowing how to extract information from encrypted data formats; (3) understanding the potential benefits and limitations of specific data sets; and (4) ascertaining the accuracy of the data sets. Some databases have not been verified with ground-based measurements, and others include inaccurate measurements that are not immediately obvious to the naive investigator (Ross & Gaffen 1998; Schroeder & McGuirk 1998). In some cases, these inaccuracies have been subsequently corrected and stored in a different database, but an interested party has to know that a revised database exists and how to locate it. Furthermore, relatively accurate climate monitoring by satellites is possible over large oceanic regions (Wentz & Schabel 2000), but accuracy is significantly reduced over land (Carleton 1991).

We avoided many of these problems by forming an alliance with individuals familiar with the use and particular idiosyncrasies of various databases and by relying on them to analyze the data for us (see papers by Alexander & Eischeid 2001; Middleton et al. 2001; Stallard 2001 [all this issue]). Unfortunately, we were unable to use as many remotely sensed data sets as we would have preferred because of various factors associated with existing databases that restricted their applicability to the questions we were asking.

Despite these problems, remotely sensed data were valuable to our project in several respects. In the case of UV-B radiation, the data from the TOMS (Total Ozone Mapping Spectrometer) satellite are the best source of information about changes in UV-B radiation over the last 20 years, the period over which many well-documented amphibian declines have occurred. Furthermore, because the amphibian die-offs in relatively undisturbed areas occurred over broad geographical regions, the use of weather models employing various types of data-gathering methods (including satellites) allowed us to compare weather patterns at a number of remote sites at which no weather stations exist. Although the size of the pixel or grid is very large in the data sets that we used (Alexander & Eischeid 2001; Middleton et al. 2001 [both this issue]), the broad geographic areas over which amphibian declines have occurred (Fig. 1) justifies the consideration of these methodologies for possible use in conservation biology.

Database on Amphibian Declines

During the planning for this project, it became clear that we needed a comprehensive database containing information on as many known geographical locations as possible,

both for which die-offs have been observed and for which no known die-offs have been documented. The Declining Amphibian Populations Task Force (DAPTF) has been gathering such information and was interested in working with us. We decided that information should be organized to serve the purposes of both our project and the DAPTF.

Considerable thought was given to exactly what information should be included. The following needs were identified: (1) environmental factors likely to be related to amphibian declines had to be described in sufficient detail that they might be useful for future investigations; (2) a set of descriptive categories had to be delineated for each site and for each species; (3) to make the data set manageable, data elements had to be reduced to those deemed absolutely critical (4) only data elements directly comparable between sites and/or species would be used.

In addition to data we gathered, we included data gathered by the DAPTF. The resulting database contains essentially all well-documented cases (i.e., published in the scientific literature) of amphibian declines and data from sites at which no declines have been observed. The data are contained in two Excel spreadsheets, the elements of which are described in Table 1. The spreadsheets were constructed with a common field by which they are linked. They can be imported into relational (or flat) database programs for analysis. The data are available electronically by request (daptf@open.ac.uk). The site spreadsheet presently contains data covering 120 sites, and the species spreadsheet contains 1200 species records. Some species are listed at several distinct sites. Those wishing to utilize the data set are reminded that some of the categories contain subjective estimates rather than hard data.

We constructed a map documenting the sites and the number of species declining per site (Fig. 1). Due to the

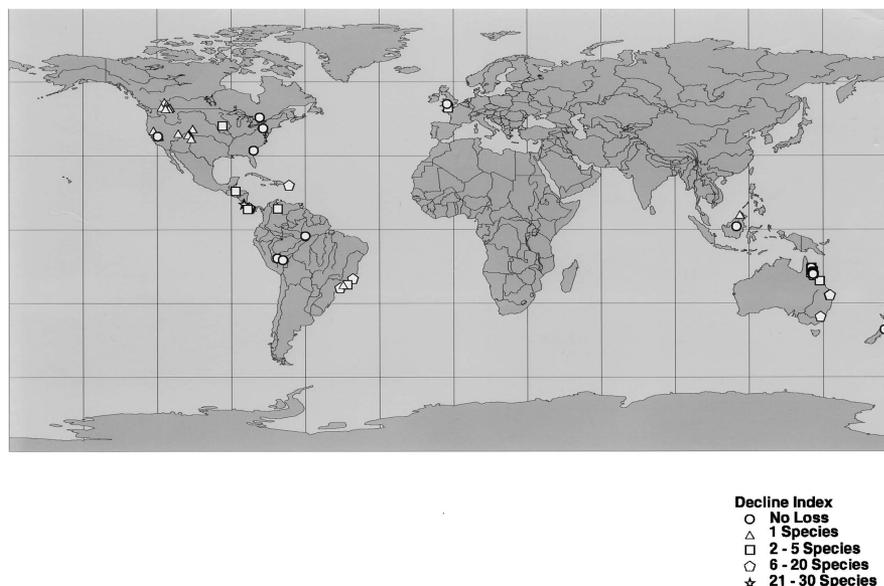


Figure 1. Summary of locations at which no declines of amphibian populations have been noted (open circles) and at which declines or extinctions have occurred.

Table 1. Data assembled for analysis of amphibian declines.

| <i>Site information</i> | <i>Species information</i> |
|--|--|
| Unique site code | unique site code |
| Site descriptor | family |
| Longitude | genus |
| Latitude | species |
| Elevation | microhabitat cover shaded? (yes/no) |
| Declines occurred at site? (yes/no) | characteristic nonbreeding habitat |
| Declines occurred after (date) | characteristic breeding habitat |
| Declines occurred before (date) | diurnal, crepuscular, nocturnal activity |
| Number of species for which decline recorded at this site | percent of decline of species |
| Number of species for which no decline recorded at this site | first date absent or definite decrease |
| Decline index* | date of last available information |
| Vegetation characteristic of site | species recovered? (yes/no) |
| Comments | life stage affected |
| | data verification source |
| | comments |

*A simple measure of the relative severity of different decline events, used to distinguish between, for example, a 20-species site at which 5 species had declined and a 4-species site at which all species had declined. Calculated for each site by dividing the square of the number of declined species by the total number of species.

scale of the map and the close proximity of many sites, not all sites in the database are pictured. No reliable observations on amphibian declines currently exist for large areas of the world, particularly Africa and Asia. New information will be added to the database as available.

Geographical Variation of Environmental Factors

The environmental variables we chose to study are particularly relevant to the observation that most of the declines in relatively undisturbed areas, such as the western United States, Costa Rica, Panama, or northeastern Queensland, occur in montane or upland areas. Mountains contain sensitive ecosystems subject to a wider range of extreme weather conditions than ecosystems at lower elevations (Beniston & Fox 1995). Each of the variables we examined changes over elevation gradients. As a result, each variable exerts different effects on amphibians at higher elevations than in geographically adjacent lowlands. For instance, air temperature decreases about 6.5° C for every 1000-m increase in elevation, when all other environmental factors are equal (Diaz & Bradley 1997). In temperate regions, summer levels of UV-B increase about 18% per 1000 m of elevational gain (Blumthaler et al. 1997). Precipitation increases with elevation on upwind slopes; rain shadows exist on downwind slopes.

Changes in the environment, caused by humans or natural processes, are predicted to affect montane ecosystems differently, and in some cases to a greater extent than ecosystems at low elevation (Beniston 1994). Although mountain ranges, particularly in the midlatitudes, generate storms and affect local climatic conditions in the adjacent lowlands, montane ecology is

expected, in turn, to be greatly effected by global climatic change (Houghton et al. 1996). Recent studies indicate that air temperatures in mountainous areas have risen significantly over the last 30 years. In temperate mountain ranges, average temperatures have increased largely because of increases in daily minimum temperatures (Diaz & Bradley 1997), and the elevation at which freezing occurs (zero degree isotherm) in tropical mountains has risen about 100 m per decade (Diaz & Graham 1996). Furthermore, as the ozone layer over the earth decreases with time and as climate changes affect cloud patterns, the potential for damaging biological effects of UV-B might also vary with elevation. Montane organisms, already under selection for high resistance to UV-B, may be affected by increasing levels of UV-B differently than those at lower elevations. Finally, deposition of airborne contaminants is greater at higher elevations than at lower ones because of orographic precipitation effects (Blais et al. 1998). Negative effects of airborne contaminants on montane ecosystems would be expected to become even more pronounced as the variety and concentrations of human-made chemicals increase.

The variables we examined are also expected to affect tropical ecosystems differently than those in temperate zones (Lips & Donnelly 2001). Because tropical ecosystems have greater species richness and ecological diversity than temperate areas, environmental change could be more devastating in tropical ecosystems than in other areas of the world. Elevations of mountain ranges and patterns of rainfall, precipitation, and climatic seasonality differ between tropical and temperate areas (see references in Lips & Donnelly 2001). Furthermore, xenobiotic compounds may also have different biological effects and persistence in the environments of tropical and temperate areas (Lacher & Goldstein 1997).

Justification of the Choice of Environmental Variables

In the roughly 350 million years of their existence, amphibians have been exposed to considerable, and probably continuous, environmental variation. Periods of relative climatic stability punctuated by rapid shifts have characterized the climatic record over the past 100,000 years (Crowley & North 1988; Taylor 1999). Variations in water chemistry, concentrations of toxins arising, for instance, from volcanic eruptions, and atmospheric conditions have also occurred during the evolutionary history of amphibians. Whether these prehistoric environmental changes caused widespread mortality of amphibian populations is unknown because both the extent of environmental variations and their effects on amphibian populations are unknown.

Temperature and Moisture Patterns

Variation in temperature and moisture patterns at our study sites were of prime interest to us in this project for several reasons: (1) Correlations between abnormal climatic patterns, such as droughts or frosts, and amphibian declines have been noted (Heyer et al. 1988; Osborne 1989; Weygoldt 1989; Ingram 1990; Pounds & Crump 1994; Stewart 1995; Laurance 1996; Pounds et al. 1999). Pounds et al. (1999) mention the possibility that climate change increases susceptibility of tropical amphibians to pathogens. (2) Temperature and water are environmental variables that play critical roles in the lives of amphibians. (3) Climatological patterns have been changing dramatically over the last 30 years (Serreze et al. 2000). We were unable to use data exclusively gathered by satellites for analyses of these variables because surface air temperatures cannot be estimated accurately over land by satellites (Carleton 1991) and because we needed records of weather patterns that predate the existence of satellite data. Accordingly, we used two data sets with information gathered from a variety of sources including satellites, weather balloons, ships, and local weather stations (Alexander & Eischeid 2001, this issue). The use of these types of models could be challenged because they lack the precision of weather monitoring at the exact site of an amphibian decline (e.g., Pounds et al. 1999). But the mass mortalities in Australia, Costa Rica–Panama, and central Colorado occurred over broad geographic areas where, in many cases, weather stations do not exist. Furthermore, these models allowed us to test whether temperature and moisture events that correlated with a die-off at one location at a given time matched those correlated with another die-off in the same geographic region at another time.

Because temperature and moisture are critical variables in the lives of amphibians, we do not believe that

normal variation in weather patterns or minor climatic shifts represent a threat to amphibians. Depending on the habitat and behavior of a given species, the range of body temperatures experienced by a given individual in a 24-hour period may extend from only a few degrees to 30° C or above (Brattstrom 1963; Carey 1978). Changes in body temperature affect virtually every aspect of amphibian life. As a general rule, biochemical, cellular, and physiological (i.e., digestion, circulation, respiration, excretion) rate functions vary two- to three-fold for every 10° C change in body temperature. The growth rate of larvae and metamorphosed young are also temperature dependent (Carey et al. 2001).

A concern of many scientists about global climate change is that current rates of temperature change may be greater than the ability of animals and plants to adapt to them (Houghton et al. 1996). Metamorphosed amphibians have many physiological and behavioral tools to cope with thermal variation. Behavioral selection of microhabitats can counteract variation in habitat temperatures (Hutchison & Maness 1979). Thermal tolerances of many terrestrial amphibians are quite broad (over a range of at least 35° C in some cases), and lethal temperatures can be raised or lowered within several days of a temperature change by metabolic acclimation to sublethal high and low temperatures, respectively (Brattstrom 1970a). Acclimatory abilities are well developed in most temperate and many tropical anurans (Brattstrom 1968). Some anurans with narrow geographic distributions and certain tropical salamanders lack the ability to acclimate themselves to thermal change (Brattstrom 1968, 1970b; Feder 1978). It is interesting that rare or more geographically limited tropical species have not declined more noticeably than more widespread, common species (Lips & Donnelly 2001). Most declining species in the United States were broadly distributed prior to decline (Carey 1993; Kagarise Sherman & Morton 1993).

Although metamorphosed individuals of many species may have the capacity to deal with rapid temperature change, amphibian eggs, larvae, and insect prey may have more restricted thermal limits, with the result that species survival would be challenged if habitat temperatures changed dramatically. Reproductive success, breeding periodicity, and food supplies are predicted to be among the features of amphibian biology most strongly affected by climate change (Donnelly & Crump 1998). Furthermore, small changes in average habitat temperatures may have a large effect on the virulence of pathogens and the effectiveness of immune defenses. For instance, an increase in body temperature of 3° C improves the immunological ability of newts (*Notophthalmus [Diemictylus] viridescens*) to reject a skin graft (Cohen 1966).

The pattern of precipitation in amphibian habitats is also a critical environmental variable because amphibians

ans lose water rapidly through their skin and their kidneys lack the ability to conserve water through production of concentrated urine (Shoemaker et al. 1992). Therefore, most amphibians are required to rehydrate frequently from a freshwater source, such as standing water or moist soil. Although many metamorphosed, terrestrial amphibians can tolerate concentration of solutes in bodily fluids and dehydration to a 40–50% loss of body mass (Shoemaker et al. 1992), eggs and larvae are particularly susceptible to dehydration. Metamorphosed individuals of species living in arid areas avoid lethal dehydration during droughts through a variety of specialized behavioral and physiological mechanisms that are not shared by amphibians living in more mesic areas (McClanahan 1967; Shoemaker & McClanahan 1975). Therefore, prolonged droughts in mesic areas could cause substantial mortality. Even if ambient moisture does not vary beyond lethal limits, foraging time can be negatively effected (Feder & Londos 1984). The effects of moderate or severe drought on pathogens and on amphibian immune defenses need investigation.

Ultraviolet-B Radiation

Considerable concern has been expressed about the world-wide decline of stratospheric ozone and the resultant increase of UV-B exposure on Earth. Although higher UV-B radiation intensities can potentially result from stratospheric ozone depletions, the UV-B levels reaching the ground can be reduced in the troposphere by either the ozone from air pollution (in industrialized areas) or by clouds (Brasseur et al. 1999). Therefore, reduction of ozone levels does not necessarily translate into higher UV-B radiation at the earth's surface. Little information is available about UV-B levels prior to 1979, but data obtained by examination of fossil pigments in lakes suggest that mid-latitude levels of UV-B between 1900–1910 may have exceeded current levels (Leavitt et al. 1997). It would be of great interest, should high UV-B radiation during the first decade of the twentieth century be confirmed, to know whether amphibian populations were affected.

We obtained data on changes in UV-B radiation at Central and South American sites of amphibian declines (Fig. 1) derived from the TOMS satellite (Middleton et al. 2001, this issue). Although the TOMS data have been available since 1979, ground verification has only recently been conducted (Herman et al. 1999; Udelhofen et al. 1999). The results of these tests indicate that the correlation between TOMS estimates and ground-based measurement varied from about 0.76 to 0.97 of the value predicted by TOMS (Udelhofen et al. 1999), the variation resulting from absorption of UV-B by cloud cover and atmospheric particles. Although the usefulness of TOMS data for research in conservation biology is restricted by the large pixel size (1° latitude by 1.25°

longitude), the lack of data prior to 1979, and other factors noted by Middleton et al. (2001, this volume), they are the only continuous data available for UV-B radiation and they are available for all locations at which amphibians have declined (Fig. 1).

Whether UV-B is playing a direct role in amphibian declines is controversial. Some studies describe significant mortality of amphibian eggs exposed to UV-B (Blaustein et al. 1994, 1995, 1996; Anazalone et al. 1998; Linzana & Padraza 1998), whereas others demonstrate no effect (Grant & Licht 1995; van de Mortel & Buttemer 1996; Nagl & Hofer 1997; Corn 1998; Crump et al. 1999) or demonstrate an effect only when UV-B exposure is coupled with low pH (Long et al. 1995).

Middleton et al. (2001, this issue) describe significant increases in UV-B radiation at sites of amphibian declines in Central and South America, but actual levels to which amphibians are exposed in these localities are unknown. If the exposure levels prove insufficient to cause direct mortality, however, it is possible that increases in sublethal exposures might affect the susceptibility of amphibians to skin infections. A number of sublethal effects of UV-B on immune function have been noted in studies of laboratory mammals, including humans (Vermeer & Hurks 1994). Damage to immune systems by UV-B can be expressed both immediately and over a period of years (i.e., skin cancers and cataracts) (Selgrade et al. 1997). In mammals, even relatively low UV-B exposure inhibits the ability of the immune system to reject tumors, contributing to the development of malignant tumors. Exposure to UV-B radiation can also limit the ability of the body to detect contact allergens and antigens, with the result that fungal, bacterial, viral, and parasitic skin infections can occur more easily than in the absence of UV-B damage (Grijzenhout et al. 1994; Norval et al. 1994; Rivas & Ullrich 1994). Despite the fact that UV-B principally affects skin organelles, systemic (whole-body) depression of immune function can result from UV-B exposure because damaged skin cells produce chemicals that have systemic immunosuppressive effects. Virtually nothing is known about the effects of sublethal UV-B exposure on the ability of amphibians to fight infection.

Atmospheric Contaminants

Industrialization of human societies and agricultural advances has resulted in the release of thousands of synthetic chemicals into the environment. The degree to which these compounds pose threats to living organisms depends on a number of factors, including the rate of breakdown or removal from the environment, bioavailability, transport, reactivity, and synergistic effects with other natural or human-made chemicals. Although direct application of toxins at sites of amphibian declines is not known to have occurred, some xenobiotic compounds are transported long distances from their sources (e.g.,

Simonich & Hites 1995; Wania et al. 1999). Although amphibian declines in Costa Rica occur primarily in upland areas in relatively pristine habitats (Lips 1998, 1999), pesticides, fungicides, herbicides, and nematicides are applied to adjacent lowland banana plantations (Castillo et al. 2000), and deposition of some of these chemicals in upland areas by orographic precipitation seems likely.

Lethal limits of several hundred xenobiotic compounds, including pesticides, industrial chemicals, and trace metals, have been evaluated for amphibians (DeVillers & Extrayat 1992; Sparling et al. 2000). Unfortunately, almost all these data were gathered through experiments with amphibian embryos and larvae rather than metamorphosed individuals, the age class dying most frequently in the field in relatively untouched environments. Documentation of exposure levels on the ground is rare for most amphibians, especially those in relatively pristine environments. The single and synergistic effects of sublethal exposure of various contaminants on immune function of amphibians are also relatively undescribed. Several studies have established that sublethal exposure to various contaminants affect other physiological and behavioral properties essential for life: this exposure caused significant increases in maintenance costs of bullfrogs (*Rana catesbeiana*) (Rowe et al. 1998) and decreased growth rates and impaired the ability of larval treefrogs (*Hyla cinerea*) to evade predators (Jung & Jagoe 1995).

We were unable to use data sets gathered by remote sensing of airborne contaminants, but Stallard (2001, this issue) used NASA data gathered by airplane to measure concentrations of airborne contaminants, such as those produced by fires, over the Caribbean. These data emphasize the fact that not only are living organisms exposed to air and rainfall carrying a variety of man-made pesticides, herbicides, fungicides, and industrial chemicals, but they are also exposed to organic chemicals, hydrogen peroxide, and organic molecules derived from smoke. Worldwide, about a half-billion hectares of land burn each year. Such large amounts of CO₂, CO, and other gases, particulates, and organic chemicals are produced from these fires that the current level of burning is thought to affect the chemistry of the troposphere, atmosphere, and global climate (Brasseur et al. 1999; Ackerman et al. 2000). But the effect of contaminants on amphibians in nature is hard to determine at present, because of the lack of information on the contaminant concentrations to which amphibians are exposed, synergistic actions of various chemicals, and physiological responses of amphibians to these exposures.

Synthesis

Some correlations exist between amphibian declines and environmental changes. Middleton et al. (2001, this

issue) found significant increases in UV-B at all 11 Central American sites of amphibian declines and smaller but significant increases at five of nine sites in South America. Significant changes in contaminant deposition have occurred in Puerto Rican streams (Stallard 2001, this issue). Stallard (2001, this issue) brought to our attention data collected over Central America and the Caribbean on airborne contaminants not formerly considered in the context of amphibian declines: the products of fires. The findings of Middleton et al. and Stallard indicate that these aspects of the environment of amphibians have changed in the last 20 years. But lack of information about exposure and tolerance levels of amphibians to these factors suggests that further research is needed before conclusions can be reached about the possible direct or indirect roles of these factors in amphibian declines. Furthermore, the lack of data extending beyond 20 years ago restricts our ability to determine how these factors might have varied in the past.

Alexander and Eischeid (2001, this issue) found that severe weather (anomalies exceeding twice the standard deviation from the long-term average) occurred in the Colorado Rockies but not at the times of amphibian declines. At the times of documented amphibian declines, the weather in the Colorado Rockies and Costa Rica did not deviate significantly from the long-term average and showed no consistent pattern during or just prior to die-offs occurring in different years. Amphibian die-offs in the tropical mountains of Australia occurred during predominantly warmer times according to one weather model but not the other. No weather patterns at the times of declines were likely to have directly caused the death of amphibians at any of our sites in these localities. If the chytrid fungus proves to be the direct cause of death at these places, the data suggest that the chytrid variants found in the tropics have different thermal optima than those in Colorado. These predictions are currently being tested.

Correlations existing between an environmental change and amphibian declines do not provide evidence of a causal relation. An animal in its environment is influenced by a variety of factors operating simultaneously. Therefore, any attempt to prove causation between changes in an environmental factor or factors and an event, such as an amphibian die-off, is fraught with difficulties because the effects of a single factor or synergistically interacting factors cannot be isolated from those of other factors operating simultaneously (Root & Schneider 1995). Because the effects of single environmental factors cannot be experimentally separated, we looked for additional types of correlations to provide a stronger case that a link might exist. For instance, we tried to evaluate environmental variables at the times and sites of amphibian declines to see whether similar events also occurred at matched sites at which no declines had occurred. If the same environmental changes occurred at

both types of sites, it would be difficult to conclude that those changes were a likely cause of amphibian declines. Attempts to find these types of correlations proved impossible. Sites at which declines had occurred could not be matched with sites where declines had not occurred because of differences in elevation, latitude, and longitude. For example, all the sites in our data set at which amphibian populations appeared to fluctuate within normal limits were at low elevation, whereas those at which populations have suffered declines were principally montane or in cold climates. The four sites at which UV-B levels did not increase in South America were at lower elevations than the five sites at which UV-B significantly increased (Middleton et al. 2001, this issue).

However, the fact that amphibian die-offs in the Colorado Rockies, the northeastern Queensland mountains, and Costa Rica and Panama were separated in both space and time presented the opportunity to examine whether an environmental phenomenon occurring just prior to or during a die-off in one location was repeated at the same time interval prior to or during die-offs at other sites within the same region. If so, a causal link might be suspected and might merit further study. Weather patterns in Central America, Australia, and Colorado differed at times of amphibian declines. Therefore, we cautiously conclude that weather is not a likely direct or indirect cause of amphibian declines at these sites.

Conclusions

The remote sensing data we used for this project enabled us to examine a variety of environmental variables in relation to known dates at specific locations of amphibian declines in ways that have not been previously possible. Our "broad-brush" approach was necessitated by the grid or pixel size of the data, but this approach allowed us to compare variables at a number of geographically separated sites. Our work with the remote-sensing data revealed some short-comings in these types of data-gathering techniques. For instance, the two weather models specified very different patterns in some cases at one locality (Alexander & Eischeid 2001, this issue). We hope, however, that this first step will stimulate further study. In particular, synergistic effects of the variables we examined need to be studied. Future research should consider the relation of these variables to other factors, such as food supply, movement of pathogens, transition of microbes from a nonpathogenic to pathogenic state, and susceptibility to infectious disease. Future research should also strive to clarify the interrelation among these phenomena with the result that we can successfully predict where the next mass amphibian die-offs will occur and, if possible, take preventive action.

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