

This work was written as part of one of the author's official duties as an Employee of the United States Government and is therefore a work of the United States Government. In accordance with 17 U.S.C. 105, no copyright protection is available for such works under U.S. Law.

Public Domain Mark 1.0

<https://creativecommons.org/publicdomain/mark/1.0/>

Access to this work was provided by the University of Maryland, Baltimore County (UMBC) ScholarWorks@UMBC digital repository on the Maryland Shared Open Access (MD-SOAR) platform.

Please provide feedback

Please support the ScholarWorks@UMBC repository by emailing scholarworks-group@umbc.edu and telling us what having access to this work means to you and why it's important to you. Thank you.

Evaluating Ultraviolet Radiation Exposure with Satellite Data at Sites of Amphibian Declines in Central and South America

ELIZABETH M. MIDDLETON,* JAY R. HERMAN,† EDWARD A. CELARIER,‡
JOHN W. WILKINSON,§ CYNTHIA CAREY,** AND ROBERT J. RUSIN††

*Laboratory for Terrestrial Physics (Code 923), Goddard Space Flight Center, National Aeronautics and Space Administration, Greenbelt, MD 20771, U.S.A., email betsym@ltpmail.gsfc.nasa.gov.

†Laboratory for Atmospheres (Code 916), Goddard Space Flight Center, National Aeronautics and Space Administration, Greenbelt, MD 20771, U.S.A.

‡Software Corporation of America, Beltsville, MD 20705, U.S.A.

§Department of Biological Sciences, The Open University, Milton Keynes MK7 6AA, United Kingdom

**Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, CO 80309, U.S.A.

††Natural Sciences Department, Bowie State University, Bowie, MD 20715, U.S.A.

Abstract: *Many amphibian species have experienced substantial population declines or have disappeared altogether during the last several decades at a number of amphibian survey sites in Central and South America. Our study addresses the use of trends in solar UV-B radiation exposure (280–320 nm) at these sites over the last two decades, derived from the Total Ozone Mapping Spectrometer satellite data. It is intended to demonstrate a role for satellite observations in determining whether UV-B radiation is a contributing factor in amphibian declines. We used these data to calculate the daily erythemal (sunburning) UV-B, or UV-B_{ery}, exposure at the latitude, longitude, and elevation of each of 20 survey sites. The annually averaged UV-B_{ery} dose, as well as the maximum values, have been increasing in both Central and South America, with higher levels reached at the Central American sites. The annually averaged UV-B_{ery} exposure increased significantly from 1979–1998 at all 11 Central American sites we examined ($r^2 = 0.60\text{--}0.79$; $p \leq 0.015$), with smaller but significant increases at five of the nine South American sites ($r^2 = 0.24\text{--}0.42$; $p \leq 0.05$). The number of days having the highest UV-B exposure ($\geq 6.75 \text{ kJ/m}^2/\text{day}$) increased in both regions from <40 days per year to approximately 58 days per year in 1998 ($r^2 = 0.24\text{--}0.42$; $p \leq 0.001$). In Central America, the contribution of these very high UV-B_{ery} exposure levels to the annual UV-B_{ery} total increased from approximately 5 to approximately 15% over the 19-year period, but actual daily exposures for each species are unknown. A UV-B ratio, the highest monthly UV-B exposure relative to the annual average for the highest UV-B category ($\geq 6.75 \text{ kJ/m}^2$), increased in both regions over this time period ($r^2 = 0.73$; $p \leq 0.001$). This UV index was consistently higher for Central America, where species declines have been the most severe. These results should justify further research into whether UV-B_{ery} radiation plays a role in amphibian population declines and extinctions. We discuss synergy among UV-B radiation and other factors, especially those associated with alterations of water chemistry (e.g., acidification) in aqueous habitats.*

Evaluación de la Exposición a la Radiación Ultravioleta con Datos de Satélite en Sitios de Declinaciones de Anfibios en Centro y Sur América

Resumen: *Muchas especies de anfibios han experimentado declinaciones poblacionales sustanciales o han desaparecido durante las últimas décadas en un número de sitios de monitoreo de anfibios en Centro y Sur América. Nuestro estudio aborda el uso de tendencias en la exposición a la radiación solar ultravioleta-B (UV-B,*

Paper submitted October 5, 2000; revised manuscript accepted January 31, 2001.

280–320 nm) en estos sitios a lo largo de las dos últimas décadas, derivadas de datos de satélite del Espectrofotómetro de Mapeo de Ozono Total. Intentamos demostrar el papel de observaciones de satélite para determinar si la radiación UV-B es un factor que contribuye a las declinaciones de anfibios. Utilizamos estos datos para calcular las exposiciones eritemales (quemadura de sol), UV-B o $UV-B_{ery}$, diarias en la latitud, longitud y altitud de cada uno de los 20 sitios de muestreo. La dosis anual promedio de $UV-B_{ery}$, así como los valores máximos, se ha incrementado tanto en Centro como en Sur América; con mayores niveles en los sitios de Centro América. Las exposiciones $UV-B_{ery}$ anuales promedio incrementaron significativamente de 1979 a 1988 en los 11 sitios que examinamos en Centro América ($r^2 = 0.60$ – 0.79 ; $p \leq 0.015$) con incrementos menores, pero significativos, en cinco de los nueve sitios de Sur América ($r^2 = 0.24$ – 0.42 ; $p \leq 0.05$). El número de días con las mayores exposiciones $UV-B_{ery}$ (≥ 6.75 kJ/m²/día) incrementó en ambas regiones de <40 días por año a ~58 días por año en 1998 ($r^2 = 0.24$ – 0.42 ; $p \leq 0.001$). En Centro América, la contribución de estos niveles muy altos de exposición $UV-B_{ery}$ al total anual de $UV-B_{ery}$ incrementó de ~5 a ~15 % a lo largo del período de 19 años, pero se desconocen las exposiciones diarias para cada especie. La proporción UV-B, la mayor exposición UV-B mensual en relación con el promedio anual para la mayor categoría UV-B (≥ 6.75 kJ/m²), incrementó en ambas regiones a lo largo de este período de tiempo ($r^2 = 0.73$; $p \leq 0.001$); este índice UV fue consistentemente mayor en Centro América donde las declinaciones de anfibios han sido más severas. Estos resultados debieran justificar más investigación sobre el papel de la radiación UV-B en la declinación y extinción de poblaciones de anfibios. Discutimos la sinergia entre la radiación UV-B y otros factores, especialmente los asociados con alteraciones de la química del agua (e. g., acidificación) en hábitats acuáticos.

Introduction

In the last two decades, observations at amphibian survey sites around the world have shown an alarming decline in populations and even total loss of species (e.g., Heyer et al. 1988; Trenerry et al. 1994; Laurance 1996; Laurance et al. 1996; Lips 1999; Houlahan et al. 2000). A recent quantitative evaluation of information compiled from many investigations corroborated that amphibian populations are declining globally and have been declining for several decades (Houlahan et al. 2000). Often, these declines have occurred in relatively undisturbed, montane environments (e.g., ≥ 500 m in elevation) over relatively short time periods of <3 years (e.g., Corn & Fogleman 1984; Heyer et al. 1988; Weygoldt 1989; Bradford 1991; Carey 1993; Lips 1998; Pounds et al. 1999). In Central and South America, most of the amphibian declines have occurred in relatively undisturbed areas in which habitat destruction, introduction of predators and competitors, or topical application of toxic chemicals are not readily apparent as causes of declines. Species in the families of Leptodactylidae (horned frogs), Bufonidae (toads), and Hylidae (tree frogs) have been the most affected.

In South America the first recorded declines occurred at three Brazilian sites in 1979; these were followed by additional declines of 1–11 species in Brazil and Venezuela between 1982 and 1990 (Heyer et al. 1988; Weygoldt 1989; Marca & Reinthaler 1993). Die-offs in Central America included 24–30 species in Costa Rica near Monteverde in 1987 (Pounds & Crump 1994; Pounds et al. 1999) and 10 species at Las Tablas in 1993 (Lips 1998), 4 species in Honduras before December 1992 (Wilson & McCranie 1993), and 1–15 species at Panamanian sites during 1996–

1997 (Lips 1999). Understanding the cause of these species losses and population declines has been identified as an important goal of the conservation biology community (Carey et al. 2001). The primary cause of death at some sites, including several Central American sites, can be attributed to infectious diseases (Scott 1993; Blaustein et al. 1994b; Berger et al. 1998; Lips 1998). It is possible that environmental changes (e.g., Phillips 1990), including warmer and drier climate conditions and changing UV-B radiation, have aided transport of pathogens into novel habitats or have increased the susceptibility of amphibians to these pathogens (Carey et al. 1999, 2001).

Changing climatic conditions have led to higher surface temperatures in montane regions in general (Diaz & Graham 1996) and in Central America in particular (Pounds et al. 1999; Still et al. 1999). Reasons for this increase include a reduction in cloudiness in Central America over the past two decades, revealed by satellite observations (Herman et al. 1999) and in recent reexaminations of climate data (Alexander & Eischeid 2001). Decreased cloud cover allows increased penetration to the Earth's surface of biologically damaging ultraviolet radiation, especially UV-B radiation between 280 and 320 nm (Caldwell 1971; Stolarski et al. 1986; Tevini & Teramura 1989). The potential UV-B exposures (i.e., the incident levels) at high elevations (e.g., mountains) are considerably greater than those at sea level (Blumthaler et al. 1997) because of shorter atmospheric path lengths for absorption by ozone and scattering by aerosols and other atmospheric constituents.

In addition to regional climate differences affecting UV-B surface exposures, there is ample evidence that chemically induced reductions in the thickness of the stratospheric ozone layer have occurred over the entire

earth (Gleason et al. 1993; Herman et al. 1993, 1996, 1999; Madronich et al. 1998) enabling higher UV-B radiation levels to reach the earth's surface (Stolarski et al. 1986; Gleason et al. 1993). Globally, UV-B radiation expressed as biologically damaging erythral UV-B ($UV-B_{ery}$) exposure increased between 1979 and 1992 by $\leq 2\%$, and approximately 6% in the Southern Hemisphere, as determined from trends in the Total Ozone Mapping Spectrometer (TOMS) satellite data (Herman et al. 1996). The smallest increases reported ($\leq 1\%$ per decade) for $UV-B_{ery}$ exposure have been associated with the 0° – $30^\circ N$ latitude band, with slightly higher estimates (1–3% per decade) for the comparable latitude band between 0° – $30^\circ S$ (Herman et al. 1996).

These zonal and global $UV-B_{ery}$ averages, however, are computed at the average elevation per TOMS pixel, which combines the relatively lower values at the surface of oceans with the higher and variable (topographic and regional) values over land areas. Therefore, zonal estimates (land plus oceans) of average $UV-B_{ery}$ exposures are associated with large statistical variances, which confound attempts to attribute statistically significant trends over time for these latitude bands (e.g., 10 – 15° wide) and for pixels in regions with changing topography (e.g., Costa Rica; Peru; Colorado [U.S.A.]) (Middleton et al. 1999). Consequently, trends showing larger increases in surface UV-B radiation have been observed with in situ measurements at ground stations than with the corresponding TOMS values for that pixel. Because $UV-B_{ery}$ increases of about 1% per year have been reported in alpine regions during the 1980s (Blumthaler & Ambach 1990) and summer increases of about 1% per year (i.e., the highest exposures, McKenzie et al. 1999) have been reported on the basis of ground monitoring stations in New Zealand in the 1990s, the TOMS zonal values should be considered conservative estimates. Most important to us, the $UV-B_{ery}$ exposures given in the standard TOMS product underestimate actual (or relative) values (but not the trends) at high elevations, a serious constraint when determinations are needed of the biologically damaging highest exposures.

The detrimental effects of UV-B radiation on life are well documented (e.g., Jagger 1985; Tevini & Teramura 1989; Tevini 1993). In many organisms, including higher plants and animals, UV-B radiation induces the production of photolyase, the DNA photorepair enzyme (Blaustein et al. 1994a, 1995, 1996, 1999; Hays et al. 1996) in epidermal tissues. Ultraviolet-B radiation also induces epidermal chemicals or structures that absorb or form a protective barrier to UV-B radiation, including skin melanin in amphibians (Little et al., unpublished data); UV-B radiation can be especially lethal to developing organisms with immature epidermal tissues (e.g., Jagger 1985). Whereas the primary result of nonlethal levels of excess UV-B radiation in plants is reduced growth and productivity (Tevini & Teramura 1989), the major effects on

older animals include the formation of tumors and suppression of the immune system (Selgrade et al. 1997).

The effects of UV-B radiation on early amphibian life stages have been examined in a number of field studies using natural versus UV-B filtered sunlight (Blaustein et al. 1994a, 1995, 1996, 1999; Hays et al. 1996; van de Mortel & Buttemer 1996; Corn 1998; Anzalone et al. 1998; Linzana & Padraza 1998). Other studies examined the effects of artificially provided "ambient" UV radiation in controlled laboratory settings (Grant & Licht 1995; Ovaska et al. 1997) or field versus laboratory "ambient" exposures (Nagl & Hofer 1997). Only a few studies have examined artificially enhanced (above ambient) UV-B levels (Long et al. 1995; Ovaska et al. 1997). No detrimental UV-B effects on embryos were found for ambient solar studies of a number of amphibian species (Grant & Licht 1995; Nagl & Hofer 1997; Corn 1998), but ambient solar UV-B exposures did reduce hatching success or survival in some species (Blaustein et al. 1994a, 1995; van de Mortel & Buttemer 1996; Anzalone et al. 1998). And, artificially applied UV-B radiation at levels 15–30% above ambient caused increased embryo mortalities and/or reduced hatching success in several species (Ovaska et al. 1997; Little et al., unpublished data), as did high UV-B irradiance (twice ambient) in combination with low pH (Long et al. 1995). Because most studies have addressed ambient UV-B exposure only, which varies considerably among studies, and because the manipulative studies with elevated UV-B levels caused significant mortalities and/or other harmful effects, we expect that the higher ambient UV-B levels of the tropics (or where regional ozone loss is high) could be harmful to the early life stages of amphibians.

We examined the magnitude of $UV-B_{ery}$ exposures and their temporal (monthly and annual) trends received at the atmosphere-vegetation interface at 20 amphibian survey sites located in Central and South America. In-depth information on these sites was obtained from an amphibian database established by the Declining Amphibian Populations Task Force (DAPTF) and from published and/or authoritatively well-documented observations from around the world (Carey et al. 2001). We used the DAPTF data base and the historical TOMS satellite data archive of the National Aeronautics and Space Administration (NASA) to address the following questions: How have $UV-B_{ery}$ exposures varied over time at the 20 Central and South American amphibian survey sites? Are $UV-B_{ery}$ exposures consistent with the regional pattern of amphibian declines?

Methods

The polar-orbiting and sun-synchronous TOMS satellite series has measured total column ozone over the entire earth, with near-complete global daily coverage from

1979 to the present, except for a nonoperational 3-year gap during 1993–1996. Midday TOMS observations are acquired within 2 hours of solar noon. The TOMS measures the sunlight scattered back from the Earth's atmosphere and surface in six narrow wavelength channels in the ultraviolet spectrum, acquiring scenes with a scanning mirror along a swath that is transverse to the orbital path. The fields of view of these scenes range in size from about 50 km near the nadir to about 200 km at the extreme off-nadir views, and these variable-sized footprints are mapped to a standard pixel grid at a spatial scale of 1° latitude by 1.25° longitude. Those pixels congruent with the geographical coordinates of the study sites (Appendices 1 & 2) were selected from the TOMS data archive.

The primary TOMS mission is to measure the total ozone concentration in the atmosphere globally, but its UV bands are also used to measure atmospheric SO_2 , aerosols, and total reflectivity of the Earth-atmosphere system (generally due to clouds or snow on the ground; Ziemke et al. 1998). Daily estimates of UV-B_{ery} exposures at the surface are much more difficult to determine than total column ozone, and the uncertainties of the estimates are due largely to assumptions made in the calculations and the limitations related to a single daily observation (e.g., cloud-cover temporal dynamics are lacking). Nevertheless, a derived data product, the daily UV-B_{ery}, is routinely produced from the TOMS data for latitudes between 65°S and 65°N (Herman et al. 1996) and added to the archive. These daily erythral exposures have original units of nanowatts per meter squared per nanometer, but, following a common practice to treat watts as dimensionless, the exposures are reported in units of joules per meter squared. Because the normalization of watts is arbitrary, the units of exposure are considered arbitrary (Herman & Celarier 1999).

Because this routine product is calculated at the average elevation per pixel, it was not suitable for this study. Therefore, we recalculated the weighted daily UV-B_{ery} exposure (joules per meter squared per day) at the Earth's surface for every available day (1979–1998) at the specific elevation of each of the 20 Central and South American sites (Appendices 1 & 2). To accomplish this, we used the original data records per pixel, the ozone and cloud cover measured by the appropriate TOMS spectral band(s); and a detailed radiative transfer code (Herman et al. 1993, 1996; Herman & Larko 1994; Herman & Celarier 1999). Site-specific data were organized, and descriptive statistics calculated, with several tailor-made “C” programs developed for this project. Data analyses were accomplished with standard software packages such as Excel (Microsoft 1998) and Systat (Statistical Product and Service Solutions 1998). The UV-B_{ery} variables determined per site included monthly means, annual means, and monthly means for 10 daily UV-B_{ery} exposure categories ($<4000 \text{ J/m}^2$; $4000\text{--}4500 \text{ J/m}^2$; $4500\text{--}5000 \text{ J/m}^2$; $5000\text{--}5500 \text{ J/m}^2$; $5500\text{--}6000 \text{ J/m}^2$; $6000\text{--}6250 \text{ J/m}^2$; 6250--

6500 J/m^2 ; $6500\text{--}6750 \text{ J/m}^2$; $6750\text{--}7000 \text{ J/m}^2$; and $>7000 \text{ J/m}^2$). We combined sites by region (Central America, South America) to compute regional trends over time for UV-B_{ery} exposures. Subsequently, individual sites were examined for temporal trends in all UV-B_{ery} variables, including a UV ratio described below. Because high UV-B_{ery} exposures are the most likely to induce biological damage or photochemical reactions, we focused on changes in the highest exposure categories. After evaluating the temporal trends in the 10 UV-B_{ery} ranges in the context of species loss and decline information, we determined that the threshold for biological damage from UV-B_{ery} exposure was $\geq 6750 \text{ J/m}^2/\text{day}$.

Examination of the DAPTF database confirmed that some of the most severe amphibian population declines and species losses have occurred in Central and South America. We calculated a species-decline index (SDI) for each survey site by DAPTF (Carey et al. 2001) as $\text{SDI} = ([\text{no. species lost}]^2 / \text{total number species})$ and used it to rank the species-loss or decline events for Central and South America; the SDI was used to roughly quantify the number of species experiencing declines relative to species richness per site. The SDI and other information synthesized from the DAPTF database for the Central and South American survey sites are summarized in Appendices 1 and 2, respectively.

Results

Regional UV-B_{ery} Analysis

We pooled the sites by region (Central America, $n = 11$; South America, $n = 9$) to compare the relative differences in UV-B_{ery} exposures for these two regions (Figs. 1–3). A definite seasonality to the UV-B_{ery} radiation exposures exists (Fig. 1). In the Central American group, the annual maximum ($\pm \text{SE}$: $6346 \pm 114 \text{ J/m}^2/\text{month}$) occurred in March, only 3 months after the November–December minimum ($4081 \pm 137 \text{ J/m}^2/\text{month}$). Lower levels were received in South America, where the annual maximum ($5710 \pm 73 \text{ J/m}^2/\text{month}$) occurred in February, 8 months after the June–July minimum ($3106 \pm 89 \text{ J/m}^2/\text{month}$). This difference in the seasonal asymmetry between the regions was especially striking, with UV levels increasing steeply between December and March in Central America, but increasing gradually from June to February in South America. These asymmetrical annual radiation distributions probably indicate a damping of the potentially higher exposure levels by clouds over the tropical rainforests of South America in the November–January period and those of Central America in the April–July period. The cloudiness regimes of these two regions also affect the timing of the monthly minima and the magnitude of the monthly maxima. Otherwise, regional differences in the month receiving the highest UV-B_{ery} exposures were due primarily to latitude.

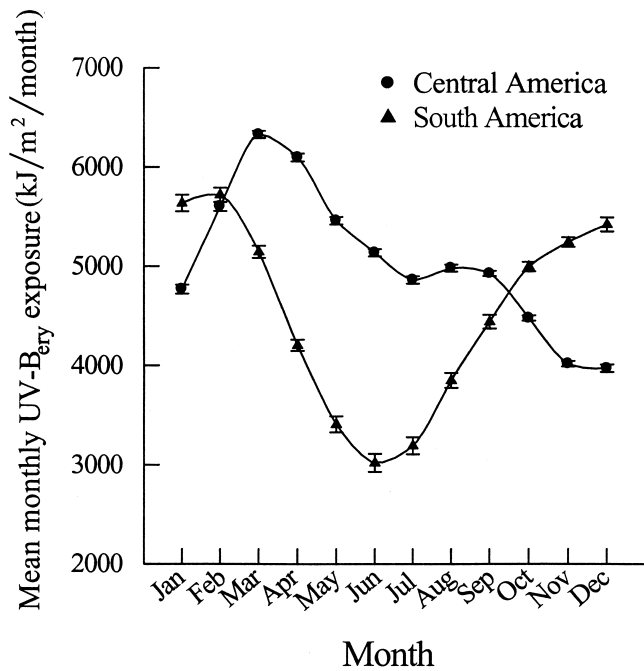


Figure 1. Sites pooled by region for the 19-year time period available from the TOMS (Total Ozone Mapping Spectrometer) record (1979–1998) to show seasonal trends in average UV-B_{ery} exposures (mean \pm SE).

We also examined regional differences (Central vs. South America) by year (Figs. 2 & 3). Although the highest month's exposures (Fig. 2a) overlapped for these two regions in many years because of site-to-site variation, the highest month (March or April) at Central American sites exceeded that of South American sites (January or February) in many individual years—1980, 1983, 1985, 1987, 1989, 1991, and 1992. Consequently, regional differences were maintained (Central > South America, 6489.7 vs. 6186.3 ± 51.5 J/m²/month; $p \leq 0.001$), whereas the magnitude of the seasonal maxima (March–April or January–February) increased significantly over the 20-year period ($r^2 = 0.55$, $n = 32$; $p \leq 0.001$).

The relative differences in the annually averaged daily UV-B_{ery} exposures between Central and South America were strongly expressed (Central > South America, $p \leq 0.001$), with the values for Central American sites being higher and less variable (5036 ± 18 J/m²/year) than those for South America (4514 ± 47 J/m²/year) over all years (Fig. 2b). The increase over time (1979–1998) for the annual means was highly significant ($r^2 = 0.89$, $n = 32$; $p \leq 0.001$, grouped by region). The upward trend was stronger for the Central American group ($r^2 = 0.56$; $n = 16$; $p = 0.001$). The greater variability ($r^2 = 0.41$, $n = 16$; $p = 0.005$) in the corresponding annual values among the South American sites (for all variables) was due primarily to a wider range of elevations in that group (Appendices 1 & 2).

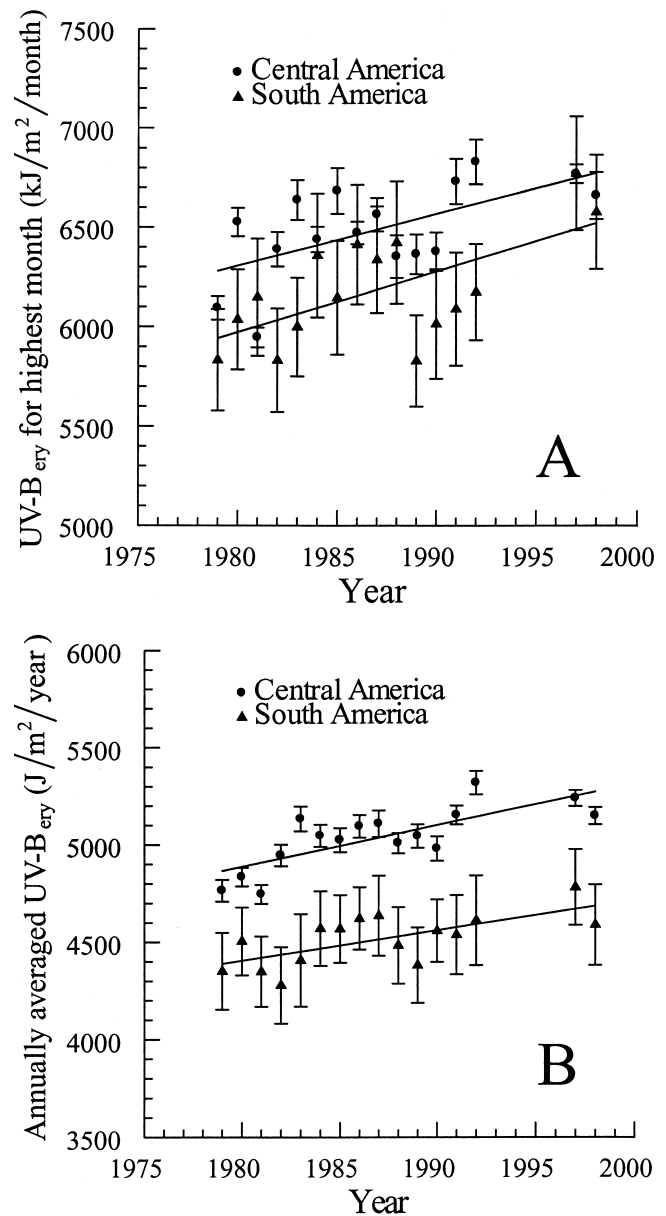


Figure 2. Sites pooled by region to examine the relative changes over the 1979–1998 period in two UV-B_{ery} parameters: (a) the highest month's average UV-B_{ery} exposure (monthly mean \pm SE) for which $r^2 = 0.55$, $n = 32$, $p \leq 0.001$; (b) the annually averaged UV-B_{ery} exposure (annual mean \pm SE) for which $r^2 = 0.89$, $n = 32$, $p \leq 0.001$.

The number of days having the highest exposures (≥ 6750 J/m²/day; Fig. 3a) increased significantly from 1979 to 1998 ($r^2 = 0.652$, $n = 32$, $p \leq 0.001$; grouped by region). The rate of increase was greater in Central America, where the number of high-radiation days per year increased substantially from an average of about 27 days in 1979 to about 58 days in 1998 ($r^2 = 0.657$, $n = 16$; $p \leq 0.001$). This increase in Central America corre-

sponds to nearly a doubling of the percentage of total UV-B_{ery} radiation attributed to this high category, from $7.7 \pm 0.8\%$ in 1979 to $12.2 \pm 0.9\%$ in 1998. In Central America, this increase in the number of high-radiation days during the dry season was responsible for the higher annual means (Fig. 3a vs. Fig. 3b) rather than an increase in the annual value for the highest exposure category (whose mean fluctuated around $7236 \pm 12 \text{ J/m}^2/\text{year}$).

In contrast, the annual average for the highest exposure category in South America ($r^2 = 0.68$, $n = 16$; $p \leq 0.001$) increased from $7213 \pm 51 \text{ J/m}^2/\text{year}$ in 1979 to $7500 \pm 97 \text{ J/m}^2/\text{year}$ in 1997–1998 (approximately 4.5% over two decades or approximately 2.2% per decade)

(Fig. 3b). The average number of high-radiation days per year varied between about 20 and 42 days, however, without clearly showing an increase over time (Fig. 3a). Consequently, the percent contribution from the highest UV-B_{ery} category was relatively stable in South America, accounting for $10.3 \pm 0.4\%$ of the annual UV-B_{ery} totals throughout the 2-decade period. Noteworthy increases occurred in both the number of high-radiation days and the annual average for the highest exposures in South America between 1982 and 1986–1987 (Fig. 3a & 3b).

The ratio of the average UV-B_{ery} exposure in the highest month (e.g., Fig. 2a) to the annual average for the highest UV-B_{ery} exposure category (e.g., Fig. 3b) was calculated

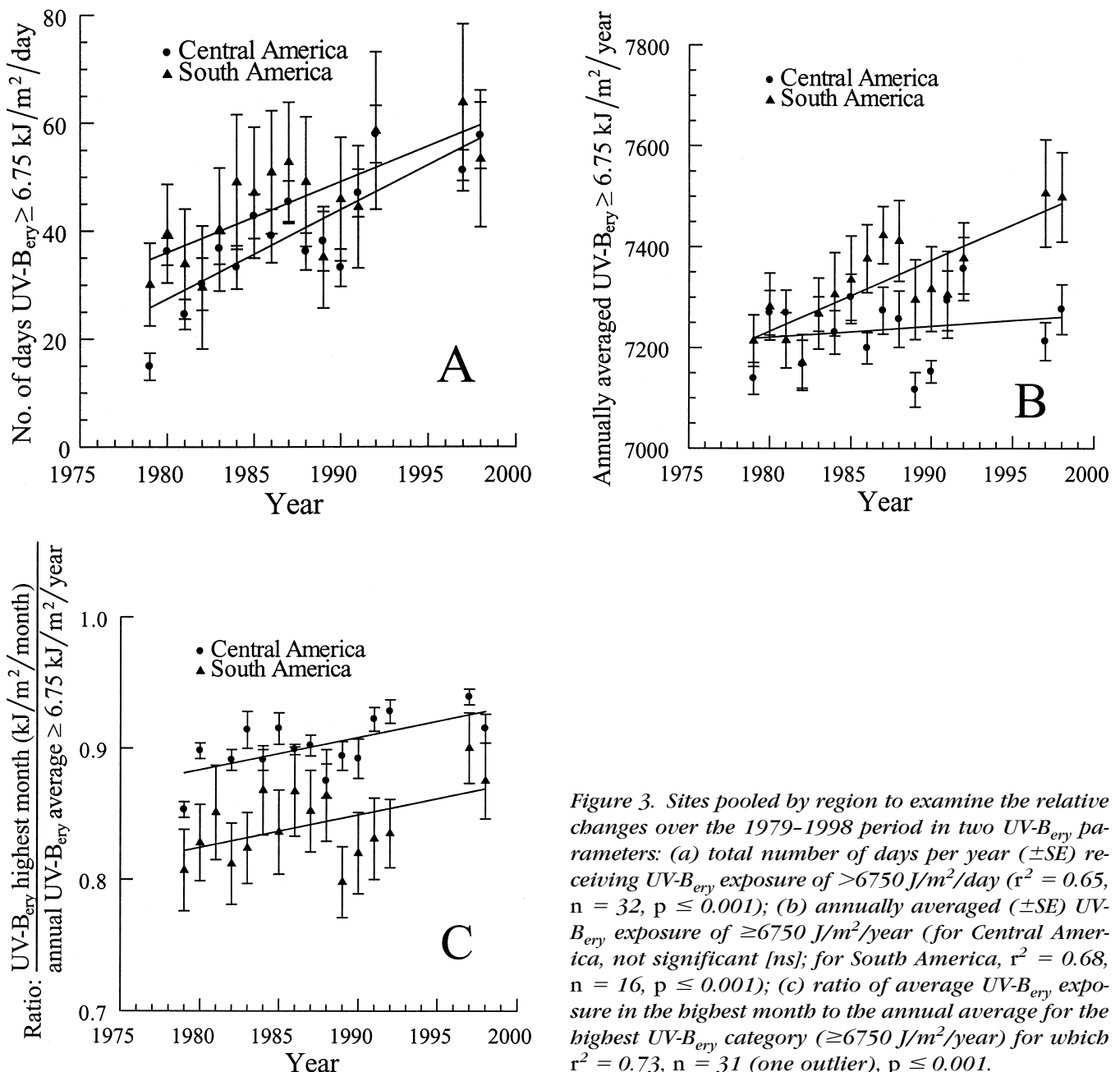


Figure 3. Sites pooled by region to examine the relative changes over the 1979–1998 period in two UV-B_{ery} parameters: (a) total number of days per year (\pm SE) receiving UV-B_{ery} exposure of $>6750 \text{ J/m}^2/\text{day}$ ($r^2 = 0.65$, $n = 32$, $p \leq 0.001$); (b) annually averaged (\pm SE) UV-B_{ery} exposure of $\geq 6750 \text{ J/m}^2/\text{year}$ (for Central America, not significant [ns]; for South America, $r^2 = 0.68$, $n = 16$, $p \leq 0.001$); (c) ratio of average UV-B_{ery} exposure in the highest month to the annual average for the highest UV-B_{ery} category ($\geq 6750 \text{ J/m}^2/\text{year}$) for which $r^2 = 0.73$, $n = 31$ (one outlier), $p \leq 0.001$.

(Fig. 3c). This ratio equals unity when all UV-B_{ery} radiation received during the highest-radiation month each year is contributed by the highest radiation category (UV-B_{ery} ≥ 6750 J/m²/day). Lower values of this ratio result when the days with the highest exposure occur frequently during months other than the highest-radiation month. In that case, UV-B_{ery} exposures during the highest-radiation month are due to substantial contributions from the next-highest radiation category (e.g., 6500 ≤ UV-B_{ery} ≤ 6750 J/m²/day). Therefore, this ratio expresses the tendency for biologically detrimental or photochemically active UV-B_{ery} exposure to be concentrated during a single month of the year. The ratio increased significantly between 1979 and 1998 ($r^2 = 0.73$, $n = 31$; $p \leq 0.001$; 1981 was an outlier for Central America) and was higher for Central than for South America (0.90 ± 0.01 and 0.84 ± 0.01 , respectively; $p \leq 0.001$). Therefore, there was a greater tendency toward a concentrated dose of radiation in the dry season in Central America during March–April than in the January–February seasonal peak in South America.

Site-Specific UV-B_{ery} Analyses

We examined several UV-B_{ery} variables separately as a function of time (1979–1998) for each site. The variable

that produced the most consistent results among sites (i.e., positive and statistically significant linear regression coefficients; retention of regional contrasts) was the annually averaged daily UV-B_{ery} exposure level (Figs. 4 & 5). All 11 Central American amphibian survey sites (Fig. 4a–i) experienced statistically significant ($p \leq 0.015$) linear increases over the 2-decade period between 1979 and 1998, which explained 60–80% of the observed variability in interannual values. In South America (Fig. 5a–i), the annually averaged daily UV-B_{ery} radiation at five of nine sites (s017, s111, s112, and s114/s115) exhibited a significant ($p \leq 0.05$) increase over time, which accounted for 40–42% of the interannual variability at two sites (s017 and s112) but <26% at the others. The three South American sites at which no amphibian declines were recorded (s010, s007, s029; Appendix 2) also exhibited little or no increase in UV-B_{ery}. All but one site of “decline” (s113) in South America exhibited a significant ($p < 0.05$) increase in UV-B_{ery} radiation over the 19-year period, and that site was nearly significant ($p = 0.06$). The UV-B_{ery} radiation may have been a contributing factor in amphibian declines because all sites with declines exhibited a trend toward higher UV-B_{ery} exposure over time, and these increases occurred during the same time period as the amphibian declines.

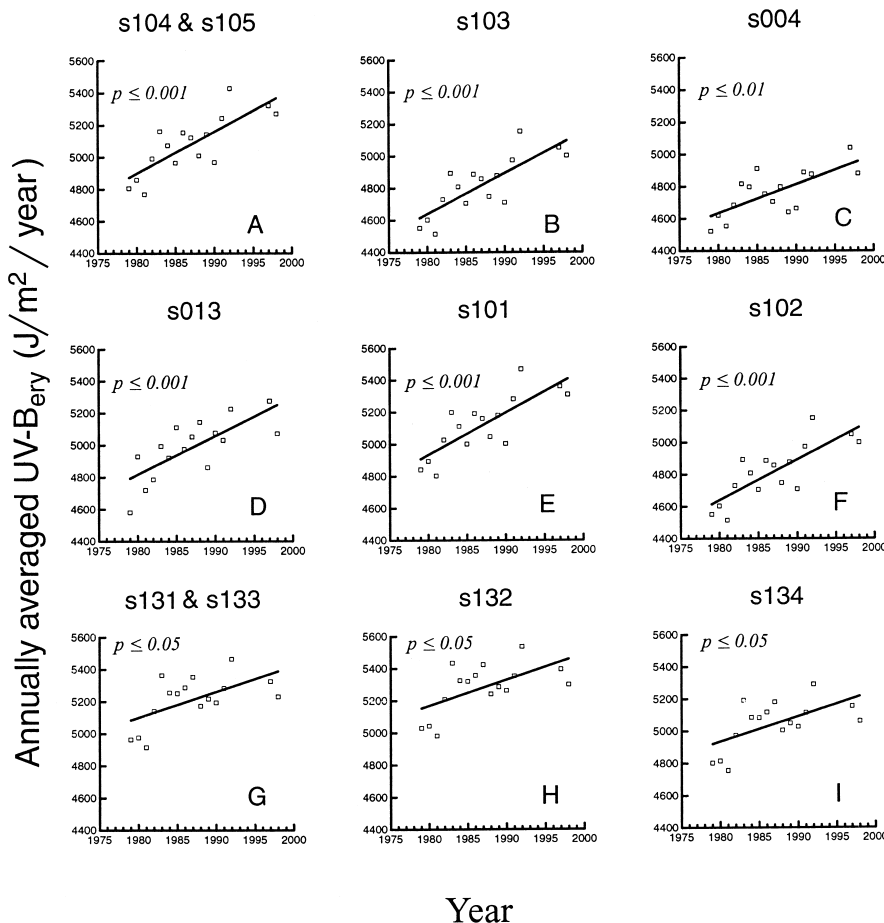


Figure 4. Annually averaged UV-B_{ery} exposure for each year available between 1979 and 1998 for the 11 Central American amphibian survey sites. Year-to-year fluctuations are given, as are the regression curves for each site (see Appendix 1 for site information). The linear increase in this UV-B_{ery} variable as a function of time is statistically significant for all sites. The *p* values indicate the significance level for the linear regressions. The statistics per site are as follows (a) $r^2 = 0.79$, $p < 0.001$; (b) $r^2 = 0.79$, $p < 0.001$; (c) $r^2 = 0.72$, $p = 0.002$; (d) $r^2 = 0.74$, $p < 0.001$; (e) $r^2 = 0.79$, $p < 0.001$; (f) $r^2 = 0.72$, $p = 0.002$; (g) $r^2 = 0.60$, $p = 0.015$; (h) $r^2 = 0.60$, $p = 0.015$; (i) $r^2 = 0.60$, $p = 0.015$.

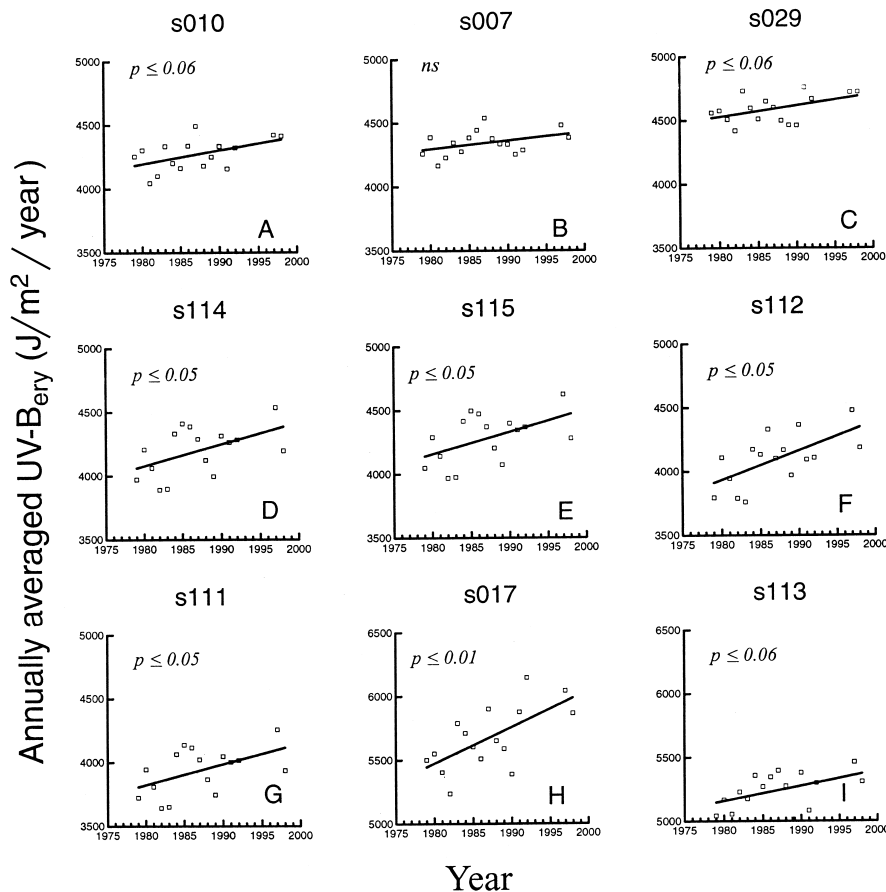


Figure 5. Annually averaged UV-B_{ery} exposure for each year for which data are available between 1979 and 1998 for the nine South American amphibian survey sites. Year-to-year fluctuations are given, as are the regression curves for each site (see Appendix 2 for site information). The linear increase in this UV-B_{ery} variable as a function of time is statistically significant ($p \leq 0.05$) for five sites. The p values indicate the significance of the linear regressions. The statistics per site are as follows (a) $r^2 = 0.24$, $p = 0.06$; (b) $r^2 = 0.14$, $p = ns$; (c) $r^2 = 0.23$, $p = 0.06$; (d) $r^2 = 0.26$, $p = 0.046$; (e) $r^2 = 0.25$, $p = 0.046$; (f) $r^2 = 0.40$, $p = 0.008$; (g) $r^2 = 0.26$, $p = 0.05$; (h) $r^2 = 0.42$, $p = 0.007$; (i) $r^2 = 0.23$, $p = 0.06$. The y-axis scale has been shifted to a higher maximum value for graphs b and i.

The species decline index (SDI) was useful for comparing the severity of die-offs among sites. In South America, species declines or losses were documented between 1979 and 1990, when SDI ranged between 0 and 5.82. In Central America, species declines or losses began in 1986 and continued at least through 1997, with the associated SDI ranging between ≤ 1 and 30.

Discussion

UV-B Effects on Amphibians

The effects of high UV-B exposure are relatively easy to quantify when they cause a reduction in survivorship. But sublethal UV-B exposures may instead induce protective responses that confound our ability to discern a UV effect. Such responses include the production of photolyase, which is correlated with hatching success or mortality among species of several genera (*Hyla*, *Rana*, and *Bufo*) (Hays et al. 1996; Blaustein et al. 1994a, 1995, 1996, 1999) and with avoidance behavior (Blaustein et al. 2000). Harmful effects of direct UV-B radiation are most likely to be associated with early life stages, with higher mortality rates for eggs laid at the water surface (Blaustein et al. 1998). Direct UV-B exposure may also

be harmful to individuals that have developed under relatively shaded conditions but are subsequently exposed to UV-B radiation (Little et al., unpublished data). This withdrawal of protective cover might be associated with seasonal cloudiness during early developmental stages followed by sustained clear skies during the dry season. Likewise, emerging metamorphs of sensitive species or populations (e.g., those having insufficient photolyase or melanin levels) may be most at risk when leaving the protection afforded by a water column or its constituents (Little et al. 2001, unpublished data). Protective cover for submerged individuals within the water column is afforded by UV-B absorbing compounds (e.g., humic acids) in the dissolved organic carbon (DOC) matter (Schindler et al. 1996; Schindler & Curtis 1997; Scully et al. 1997; Little et al. 2001, unpublished data). The DOC is produced from degradation of vegetation, especially abundant in tropical ecosystems.

Most, if not all, species experiencing declines or losses in Central America live near streams, with adults active primarily in the shade or at night (Lips 1998, 1999); data are limited on declining South America species. Consequently, the effects of indirect UV-B radiation may be more important in tropical ecosystems than those produced by direct exposure in open habitats. For example, UV-B radiation may harm the amphibian food supply

(e.g., mosquitoes; Mims et al. 1997) or alter the habitability of their breeding ponds. Where UV-B radiation penetrates the water column, chemical reactions occur that reduce DOC (Scully & Lean 1994; Lean 1997) and increase production of biologically harmful photochemical by-products such as hydrogen peroxide, singlet oxygen, and carbon monoxide (Scully et al. 1997). These photochemical processes are enhanced by higher temperatures (Schindler et al. 1996; Schindler & Curtis 1997).

Acidification of aqueous ecosystems also decreases DOC, allowing higher UV-B at depth (Yan et al. 1996). Consequently, acidification of warm tropical breeding ponds may cause them to be essentially devoid of protective DOC and may contribute noxious compounds to and facilitate penetration of UV-B radiation into the water column. Acid aerosols from biomass burning could elevate the acidity of upland streams and ponds. The pervasive and global extent of pollution plumes, especially particulates (e.g., soot), was recently implicated in climate changes (Hansen et al. 2000). Although our survey sites in Central and South America were largely in “relatively undisturbed” areas, increases in a nitric-sulfuric acid aerosol, primarily from fires associated with deforestation, were observed in air sampled by NASA over Costa Rica and Panama (Stallard 2001). The toxicity of these wind-borne pollutants could be enhanced by UV-B-induced photochemical reactions on particles adhering to water droplets in the air or the mist that envelopes cloud forests, eventually reaching amphibian water habitats. Even low UV-B exposures (<5% of surface) can increase the potency of harmful water-borne pollutants. For example, the toxicity of a common forest insecticide (carbonyl) increased 12-fold for *Hyla* tadpoles (Zaga et al. 1998), and the toxicity of a petroleum product increased 4-fold for *Rana* tadpoles (Little et al. 2001). Moreover, a combined effect of ambient UV-B, excess nitrate, and low pH in breeding ponds on the survival and activity of *Rana* larvae has been reported recently (Hatch & Blaustein 2000).

Because the most likely cause of amphibian mass mortalities in the tropical mountains of Costa Rica, Panama, and Australia is infection by *Chytridiomycosis* (Berger et al. 1998; Daszak et al. 1999), the possibility that higher UV-B levels contribute indirectly to the success of this fungus against amphibian skin defenses needs further research. Synergy between a pathogenic fungus and UV-B radiation has increased mortality among amphibian embryos more than either factor alone (Kiesecker & Blaustein 1995), although not all species were affected and explanations for the differential responses are needed.

Increases in UV-B_{ery} Exposures and Amphibian Species Losses

The tropical rainforests of Costa Rica, Panama, and Australia have experienced the most severe amphibian pop-

ulation declines over the last two decades (Trenerry et al. 1994; Lips 1998, 1999). The relative effect of losing a few (e.g., 1 of 2) species at temperate sites can have as great or greater an effect as losing many (e.g., 5 of 10) species at tropical sites with high species richness. The SDI provides a measure of the proportion of resident species affected by declines. We showed that several UV-B_{ery} exposure variables increased over 20 years at sites of amphibian declines in Central and South America and that these variables did not increase significantly at the few low-elevation sites at which no declines have been recorded.

Differences in UV-B_{ery} exposure between Central and South America were consistent with the regional differences in species losses and declines. Sites in Central America had higher average annual UV-B_{ery} exposure, higher maximum-month UV-B_{ery} exposure, a higher percentage of the annual dose from the highest exposure category, a faster transition each year from lowest to highest UV-B_{ery} levels, and a greater number of amphibian species and declining species (Appendices 1 & 2). Declines involving the most species at the Central American sites (Appendix 1) occurred in concert with an exceptionally high UV-B_{ery} dose for ≥ 2 years in short succession at a particular site. If UV-B_{ery} exposure facilitates species declines, the severity of these declines are probably influenced by more than the magnitude of the UV-B_{ery} exposure. In addition to the actual exposure levels, the timing and duration of high-radiation events during the annual cycle, relative to the typical “background” exposure levels, might accentuate or, conversely, ameliorate the receipt of high exposures. We are currently evaluating this possibility and extending our analysis to amphibian survey sites in other regions, such as Australia and North America.

Limitations and Errors Inherent in Data Sources

Although it is as comprehensive and complete as possible, the valuable information in the database on declining amphibian populations (Carey et al. 2001) relies on observations and measurements from many sources. Because these data and observations were compiled post hoc from field research originally conducted in the context of ongoing biological programs to address diverse amphibian population questions, they are not necessarily consistent in information type, time scale, accuracy, or quality among sites. In many cases, the available information is already out of date. In retrospect, we find that the lack of a standard set of comprehensive field measurements and observations that includes the monitoring of environmental variables such as temperature, precipitation, radiation, and water chemistry hinders our ability to unravel the problem at hand.

The calculated index of species effect, the SDI, is also imperfect. The intent behind its formulation was to de-

scribe quantitatively the relative effect of species declines per locale. It is far easier to ascertain which species are missing, or whose populations are severely reduced, by comparing current with previous recorded levels than it is to enumerate the total species present at any time. This is especially true for rare species, those with small individuals, or those whose resident populations are small in number. Because the total number of species is the denominator term of the SDI, this index may provide an overestimate of "effect" for sites where information on unaffected species is not available. The sites for which information on unaffected (i.e., nondeclining) species is unavailable include the four sites in Central America with SDI of ≤ 4 and four sites in South America with SDI between ≤ 1 and 5. None of the sites having high losses or declines, or those with zero declines, is in dispute; the uncertain sites all fall into the mid-impact range ($\sim 1 \leq \text{SDI} \leq 5$). For each of these eight sites, a lower index would result from incorporation of additional species into the denominator term, yielding a lower SDI value. Consequently, the current SDI, though imperfect, is still a useful first approximation.

The large size of the satellite pixel (50–200 km across) and the necessary assumption of a homogeneous atmosphere within that pixel limits our ability to calculate independent UV-B_{ery} exposure for specific sites at the same elevation within any grid cell. This means that UV-B_{ery} exposures determined for multiple sites at different elevations within a single TOMS pixel are correlated, exhibiting the same trends over time. Actual within-pixel (or site-to-site) differences in atmospheric clarity (e.g., cloudiness, aerosols) which naturally occur at local scales are averaged in the TOMS values. Consequently, UV-B_{ery} exposure determined on any given day from TOMS data co-located with the survey sites may be overestimated or underestimated, depending on the relative agreement of the atmospheric clarity above a particular survey site to the regionally averaged atmospheric clarity of the pixel. The algorithm does not take into account absorbing aerosols, such as those produced from biomass burning.

Because TOMS makes measurements over a site only once a day, within ± 2 hours of solar noon, the calculated exposures may not accurately represent actual daily exposures at sites where there is significant diurnal variation in cloud cover. This also means that UV-B_{ery} exposures determined from satellite measurements may not match similar measurements acquired from a stationary ground-based instrument placed at a single point. But TOMS data should provide a more systematic and stable estimate over time than ground-based point measurements. A recent high-latitude comparison indicates that calculated TOMS exposures can yield a $\geq 20\%$ overestimate of actual UV-B radiation determined by a ground-based point sensor (Herman et al. 1999). Nevertheless, Udelhofen et al. (1999) report correlations be-

tween TOMS values and ground-based measurements at eight stations of 0.76–0.97, with most > 0.93 . We are not concerned about whether TOMS data overestimate surface UV-B_{ery} exposure, although accurate determination of the threshold-producing biological damage is essential, as long as the temporal trends in the relative doses are accurate. The most important factor is that satellite data have provided an invaluable information source describing the historical record and continue to provide an ongoing and current record of the three-dimensional spatial (latitude, longitude, and elevation) and temporal distributions of UV-B_{ery} exposures in Central and South America. Although higher spatial resolution is desirable, the existing and continuing TOMS data provide characteristics unavailable from field data: standard, stable, and global measurement of a critical environmental parameter, UV-B_{ery} exposure.

Synergy between UV-B Radiation, Related Climate Changes, and Human Influences

Low-latitude montane regions receive some of the highest UV-B_{ery} exposures on Earth (e.g., Costa Rica), increasing or not. The relevant issue may not be whether UV-B_{ery} exposures have increased over the past decades, but whether contemporary levels are adequate, in conjunction with air-borne pollutants, to activate harmful photochemical processes in rain/mist or ponds that negatively affect amphibian health and survival. We found that UV-B_{ery} exposure may be sufficiently high to participate in the chain of events that produce unsuitable amphibian habitats. The relatively high dose (e.g., the ratio described in Fig. 3c) may describe a biologically relevant parameter in these tropical and subtropical systems which increased significantly in both Central and South America. But the highest exposure category (alone) significantly increased in South America (but not in Central America) over the last 2 decades by approximately 4.5% (or approximately 2.2% per decade). This is equivalent to the rate of increase determined for the highest exposure category associated with another amphibian decline site in the mountains of Colorado (U.S.A.). Also, this TOMS estimate of the upward trend in UV-B_{ery} exposure is similar to the TOMS zonal average that includes Central America ($\leq 3\%$ per decade, based on all data, not just the highest category). These decadal or annual trend estimates derived from TOMS observations are considerably lower than comparable trends determined from ground-based measurements reported by some investigators (e.g., Blumthaler & Ambach 1990; McKenzie et al. 1999), but there are no known long-term UV-B radiation ground-monitoring stations in Central America for comparison. The TOMS reflectivity data in the cloud-detection wavebands (380 or 360 nm) reveal that mid-day cloud cover over Central America from 1979 to 1998 decreased (in agreement with the findings of Alexander

and Eischeid [2001] and Herman et al. [1999]). Therefore, the resulting increases in UV-B_{ery} exposure are due to both reduced mid-day cloudiness and a small upward trend in ozone loss that has occurred and is still occurring globally.

All evidence that supports a role for climatic parameters in amphibian species declines is correlative and/or circumstantial. Our results suggest a statistically significant increase in UV-B_{ery} exposure at many Central and South American decline sites and are generally compatible with observed climate changes involving higher temperatures and reduced precipitation implicated in some amphibian declines (Pounds et al. 1997, 1999). A lower incidence of cloud cover is associated with reduced rainfall and sustained high-radiation periods (including higher UV-B_{ery} exposures) in the ecosystems supporting amphibians. High-radiation periods, especially when coupled with higher temperatures, would foster evaporation from water surfaces during periods of drought, possibly concentrating noxious compounds, whether pollutants or photochemical reaction products.

At the Puerto Rican amphibian decline site (s013), UV-B_{ery} exposure significantly increased according to our TOMS data. At the same time, rainfall declined and drought periods and acid aerosols increased. Temperature data, however, show no significant trends (Stallard 2001). The latter result contrasts with the situation in Costa Rica, where elevated temperatures (Still et al. 1999) correlate with the timing of local declines (Pounds et al. 1999). A re-analysis of climate variation in Costa Rica and Panama (Alexander & Eischeid 2001) found that temperature and precipitation anomalies fell within the normal range of variability and are unlikely the direct cause of amphibian declines. Because most chemical reactions are temperature-dependent, typically with greater rates at higher temperatures (Rome et al. 1992), photochemical reactions associated with UV-B radiation and aerosol and pollutant transport in tropical systems could be augmented in Central and South America. If this is so, then the effects could exceed those observed in temperate and boreal systems, with associated reductions in pH and dissolved organic carbon (DOC) and increased UV-B transmission and toxicity of pollutants or photochemical byproducts. The combined effects of a three-factor synergistic interaction—elevated levels of UV-B radiation, acid pollutants, and temperature—facilitate acidification of aqueous habitats or low-lying clouds (e.g., in cloud forests), creating a stressful environment that weakens immune-system responses, thus possibly enabling fungal infections and contributing indirectly to amphibian declines. This hypothesis deserves further study.

The problem of separating human effects from natural population fluctuations is complex (Pechmann et al. 1991; Blaustein et al. 1994c; Pechmann & Wilbur 1994). Because multiple factors are most likely responsible for amphibian declines, studies involving single factors can-

not address that complexity, as discussed by Kiesecker and Blaustein (1995). Ultimately, climate changes are linked to anthropogenic activities occurring both nearby (e.g., tropical biomass burning, fossil fuel combustion) and far away (e.g., continued use of chlorofluorocarbons, atmospheric dust, and aerosol transport). We propose that satellite-based investigations, in conjunction with in situ observations, will foster understanding of species and population declines around the world.

Acknowledgments

This research was supported by National Aeronautics and Space Administration (NASA) grant NAG8-1412 (designated code 616016). The authors thank B. W. Mee-son (NASA/GSFC, Code 900) for her role in facilitating the creation of the Amphibian Decline Data Base and for enabling the institutional links.

Literature Cited

- Alexander, M. A., and J. K. Eischeid. 2001. Climate variability in regions of amphibian declines. *Conservation Biology* **15**:930–942.
- Anzalone, C. R., L. B. Kats, and M. S. Gordon. 1998. Effects of solar UV-B radiation on embryonic development in *Hyla cadaverina*, *Hyla regilla*, and *Taricha torosa*. *Conservation Biology* **12**:646–653.
- Berger, L., R. Speare, P. Daszak, D. E. Green, A. A. Cunningham, C. L. Goggin, R. Slocumbe, M. A. Ragan, A. D. Hyatt, K. R. McDonald, H. B. Hines, K. R. Lips, G. Marantelli, and H. Parkes. 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rainforests of Australia and Central America. *Proceedings of the National Academy of Sciences of the United States of America* **95**:9031–9036.
- Blaustein, A. R., P. D. Hoffman, D. G. Hokit, J. M. Kiesecker, S. C. Walls, and J. B. Hays. 1994a. UV repair and resistance to solar UV-B in amphibian eggs: a link to population declines? *Proceedings of the National Academy of Sciences of the United States of America* **91**:1791–1795.
- Blaustein, A. R., D. G. Hokit, R. K. O'Hara, and R. A. Holt. 1994b. Pathogenic fungus contributes to amphibian losses in the Pacific Northwest. *Biological Conservation* **67**:251–254.
- Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994c. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology* **8**:60–71.
- Blaustein, A. R., B. Edmond, J. M. Kiesecker, J. J. Beatty, and D. G. Hokit. 1995. Ambient ultraviolet radiation causes mortality in salamander eggs. *Ecological Applications* **5**:740–743.
- Blaustein, A. R., P. D. Hoffman, J. M. Kiesecker, and J. B. Hays. 1996. DNA repair activity and resistance to solar UV-B radiation in eggs of the red-legged frog. *Conservation Biology* **10**:1398–1402.
- Blaustein, A. R., J. M. Kiesecker, D. P. Chivers, D. G. Hokit, A. Marco, L. K. Belden, and A. Hatch. 1998. Effects of ultraviolet radiation on amphibians: field experiments. *American Zoologist* **38**:799–812.
- Blaustein, A. R., P. D. Hoffman, D. P. Chivers, J. M. Kiesecker, W. P. Leonard, A. Marco, D. H. Olson, J. K. Reaser, and R. G. Anthony. 1999. DNA repair and resistance to UV-B radiation in western spotted frogs. *Ecological Applications* **9**:1100–1105.
- Blaustein, A. R., D. P. Chivers, L. G. Kats, and J. M. Kiesecker. 2000. Effects of ultraviolet radiation on locomotion and orientation in roughskin newts (*Taricha granulosa*). *Ethology* **106**:227–234.
- Blumthaler, M., and W. Ambach. 1990. Indication of increasing solar ultraviolet-B radiation flux in alpine regions. *Science* **248**:206–208.

- Blumthaler, M., W. Ambach, and R. Ellinger. 1997. Increase in solar UV radiation with altitude. *Journal of Photochemistry and Photobiology [B: Biology]* **39**:130–134.
- Bradford, D. F. 1991. Mass mortality and extinction in a high-elevation population of *Rana muscosa*. *Journal of Herpetology* **25**:174–177.
- Caldwell, M. M. 1971. Solar UV irradiation and the growth and development of higher plants. Pages 131–177 in A. C. Giese, editor. *Photophysiology* 6. Academic Press, New York.
- Carey, C. 1993. Hypothesis concerning the causes of the disappearance of boreal toads from the mountains of Colorado. *Conservation Biology* **7**:355–362.
- Carey, C., N. Cohen, and L. Rollins-Smith. 1999. Amphibian declines: an immunological perspective. *Developmental and Comparative Immunology* **23**:459–472.
- Carey, C., H. R. Heyer, J. Wilkinson, R. A. Alford, P. Arntzen, L. Hungerford, K. R. Lips, E. M. Middleton, S. Orchard, J. A. Pounds, and A. S. Rand. 2001. Amphibian declines and environmental change: use of remote-sensing data to identify environmental correlates. *Conservation Biology* **15**:903–913.
- Corn, P. S. 1998. Effects of ultraviolet radiation on boreal toads in Colorado. *Ecological Applications* **8**:18–26.
- Corn, P. S., and J. C. Fogleman. 1984. Extinction of montane populations of the northern leopard frog (*Rana pipiens*) in Colorado. *Journal of Herpetology* **18**:147–152.
- Daszak, P., L. Berger, A. A. Cunningham, A. D. Hyatt, D. E. Green, and R. Spear. 1999. Emerging infectious diseases and amphibian population declines. *Emerging Infectious Diseases* **5**:735–748.
- Diaz, H. F., and N. E. Graham. 1996. Recent changes in tropical freezing heights and the role of sea surface temperatures. *Nature* **383**:152–155.
- Gleason, J. F., P. K. Bhartia, J. R. Herman, R. McPeters, P. Newman, R. S. Stolarski, L. Flynn, G. Labow, D. Larko, C. Seftor, C. Wellenmeyer, W. D. Komhyr, A. J. Miller, and W. Planet. 1993. Record low global ozone in 1992. *Science* **260**:523–526.
- Grant, K. P., and L. E. Licht. 1995. Effects of ultraviolet radiation on life-history stages of anurans from Ontario, Canada. *Canadian Journal of Zoology* **73**:2292–2301.
- Hansen, J., M. Sato, R. Ruedy, A. Lacis, and V. Oinas. 2000. Global warming in the twenty-first century: an alternative scenario. *Proceedings of the National Academy of Sciences of the United States of America* **97**:9875–9880.
- Hatch, A. C., and A. R. Blaustein. 2000. Combined effects of UV-B, nitrate, and low pH reduce the survival and activity level of larval cascades frogs (*Rana cascades*). *Archives of Environmental Contamination and Toxicology* **39**:494–499.
- Hays, J. B., A. R. Blaustein, J. M. Kiesecker, P. D. Hoffman, I. Pandelova, D. Coyle, and T. Richardson. 1996. Development responses of amphibians to solar and artificial UV-B sources: a comparative study. *Photochemistry and Photobiology* **64**:449–456.
- Herman, J. R., and E. A. Celarier. 1999. Erythral exposure data product, TOMS user guide. Technical publication. National Aeronautics and Space Administration, Goddard Space Flight Center, Greenbelt, Maryland.
- Herman, J. R., and D. Larko. 1994. Low ozone amounts during 1992–1993 from Nimbus 7 and Meteor 3 total ozone mapping spectrometers. *Journal of Geophysical Research* **99**:3483–3496.
- Herman, J. R., R. D. McPeters, and D. Larko. 1993. Ozone depletion at northern and southern latitudes derived from January 1979 to December 1991 total ozone mapping spectrometer data. *Journal of Geophysical Research* **98**:12783–12793.
- Herman, J. R., P. K. Bhartia, J. Ziemke, Z. Ahmad, and D. Larko. 1996. UV-B increases (1979–1992) from decreases in total ozone. *Geophysical Research Letters* **23**:2117–2120.
- Herman, J. R., N. Krotkov, E. Celarier, D. Larko, and G. Labow. 1999. Distribution of UV radiation at the Earth's surface from TOMS-measured UV-backscattered radiances. *Journal of Geophysical Research* **104**:12,059–12,076.
- Heyer, W. R., A. S. Rand, C. A. Goncalves da Cruz, and O. L. Peixoto. 1988. Decimations, extinctions, and colonizations of frog populations in southeast Brazil and their evolutionary implications. *Biotropica* **20**:230–235.
- Houlahan, J. E., C. S. Findlay, B. R. Schmidt, A. H. Meyer, and S. L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. *Nature* **404**:752–755.
- Jagger, J. 1985. *Solar-UV actions on living cells*. Praeger Publishers, New York.
- Kiesecker, J. M., and A. R. Blaustein. 1995. Synergy between UV-B radiation and a pathogen magnifies amphibian embryo mortality in nature. *Proceedings of the National Academy of Sciences of the United States of America* **92**:11049–11052.
- Laurance, W. F. 1996. Catastrophic declines of Australian rainforest frogs: Is unusual weather responsible? *Biological Conservation* **77**:203–212.
- Laurance, W. F., K. R. McDonald, and R. Speare. 1996. Epidemic disease and the catastrophic decline of Australian rain forest frogs. *Conservation Biology* **10**:406–413.
- Lean, D. R. S. 1997. Influence of ultraviolet-B radiation on aquatic ecosystems. Pages 1–20 in E. E. Little, editor. *Environmental toxicology and risk assessment: ASTM STP 1333*, 7. American Society for Testing and Materials, West Conshohocken, Pennsylvania.
- Linzana, M., and E. M. Padraza. 1998. The effects of UV-B radiation on toad mortality in mountainous areas of central Spain. *Conservation Biology* **12**:703–707.
- Lips, K. R. 1998. Decline of a tropical montane amphibian fauna. *Conservation Biology* **12**:106–117.
- Lips, K. R. 1999. Mass mortality and population declines of anurans at an upland site in western Panama. *Conservation Biology* **13**:117–125.
- Little, E. E., R. D. Calfee, C. Cleveland, R. Skinker, A. Zaga-Parkhurst, and M. Barron. 2001. Photoenhanced toxicity in amphibians: synergistic interactions of solar ultraviolet radiation and aquatic communities. *Journal of the Iowa Academy of Sciences* **107**:67–71.
- Long, L. E., L. S. Saylor, and M. E. Soule. 1995. A pH/UV-B synergism in amphibians. *Conservation Biology* **9**:1301–1303.
- Madronich, S., R. L. McKenzie, L. O. Björn, and M. M. Caldwell. 1998. Changes in biologically active ultraviolet radiation reaching the Earth's surface. *Journal of Photochemistry and Photobiology* **46**:5–19.
- Marca, E. L., and H. P. Reinharter. 1993. Population changes in *Atelopus* species of the Cordillera de Merida, Venezuela. *Herpetology Reviews* **22**:125–128.
- McKenzie, R. L., B. Conner, and G. Bodecker. 1999. Increased summertime UV radiation in New Zealand in response to ozone loss. *Science* **285**:1709–1711.
- Middleton, E. M., J. R. Herman, E. A. Celarier, and R. J. Rusin. 1999. Trends in ultraviolet radiation at the Earth's land surfaces determined from two decades of satellite-based total Ozone Mapping Spectrometer (TOMS) observations. Four pages in *Proceedings, 1999 International geoscience and remote sensing symposium. Session DD08(2), atmospheric sounding*. CD volume 4. Institute of Electrical and Electronic Engineers, Geoscience and Remote Sensing Society. Piscataway, New Jersey.
- Mims, F. M., B. N. Holben, T. F. Eck, B. C. Montgomery, and W. B. Grant. 1997. Smoky skies, mosquitoes, and disease. *Science* **276**:1774–1775.
- Nagl, A. M., and R. Hofer. 1997. Effects of ultraviolet radiation on early larval stages of the alpine newt, *Triturus alpestris*, under natural and laboratory conditions. *Oecologia* **110**:514–519.
- Ovaska, K., T. M. Davis, and I. Novales Flamarique. 1997. Hatching success and larval survival of the frogs *Hyla regilla* and *Rana aurora* under ambient and artificially enhanced solar ultraviolet radiation. *Canadian Journal of Zoology* **75**:1081–1088.
- Pechmann, J. H. K., and H. M. Wilbur. 1994. Putting declining amphibian populations in perspective: natural fluctuations and human impacts. *Herpetologia* **50**:65–84.
- Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* **253**:892–895.

- Phillips, K. 1990. Where have all the frogs and toads gone? *BioScience* **40**:422–424.
- Pounds, J. A., and M. L. Crump. 1994. Amphibian declines and climate disturbance: the case of the golden toad and the harlequin frog. *Conservation Biology* **8**:72–85.
- Pounds, J. A., M. P. L. Fogden, J. M. Savage, and G. C. Gorman. 1997. Tests of null models for amphibian declines on a tropical mountain. *Conservation Biology* **11**:1307–1322.
- Pounds, J. A., M. P. L. Fogden, and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. *Nature* **398**:611–615.
- Rome, L. C., E. D. Stevens, and H. B. John-Alder. 1992. The influence of temperature and thermal acclimation on physiological function. Pages 183–205 in M. E. Feder and W. W. Burggren, editors. *Environmental physiology of the amphibia*. University of Chicago Press, Chicago.
- Schindler, D. W., and P. J. Curtis. 1997. The role of DOC in protecting freshwaters subjected to climatic warming and acidification from UV exposure. *Biogeochemistry* **36**:1–18.
- Schindler, D. W., P. J. Curtis, B. R. Parker, and M. P. Stainton. 1996. Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. *Nature* **379**:705–708.
- Scott, N. 1993. Post-metamorphic death syndrome. *Froglog* **7**:1–2.
- Scully, N. H., and D. R. S. Lean. 1994. The attenuation of ultraviolet radiation in temperate lakes. *Archiv fur Hydrobiologie Beiheft* **43**:135–144.
- Scully, N. H., W. F. Vincent, D. R. S. Lean, and W. J. Cooper. 1997. Implications of ozone depletion for surface-water photochemistry: sensitivity of clear lakes. *Aquatic Sciences* **59**:260–274.
- Selgrade, M. K., M. H. Rapacholi, and H. S. Koren. 1997. Ultraviolet radiation-induced immune modulation: potential consequences for infectious, allergic, and autoimmune diseases. *Environmental Health Perspectives* **105**:332–334.
- Stallard, R. F. 2001. Possible environmental factors underlying amphibian decline in eastern Puerto Rico: analysis of U.S. government data archives. *Conservation Biology* **15**:943–953.
- Still, C. J., P. N. Foster, and S. H. Schneider. 1999. Simulating the effects of climate change on tropical montane cloud forests. *Nature* **398**:608–610.
- Stolarski, R. S., A. J. Krueger, M. R. Schoeberl, R. D. McPeters, P. A. Newman, and J. C. Alpert. 1986. Nimbus 7 satellite measurements of the springtime Antarctic ozone decrease. *Nature* **322**:808–810.
- Tevini, M. 1993. UV-B radiation and ozone depletion. Lewis Publishers, Boca Raton, Florida.
- Tevini, M., and A. H. Teramura. 1989. UV-B effects on terrestrial plants. *Photochemistry and Photobiology* **50**:479–487.
- Trenerry, M. P., W. F. Laurance, and K. R. McDonald. 1994. Further evidence for the precipitous decline of endemic rainforest frogs in tropical Australia. *Pacific Conservation Biology* **1**:150–153.
- Udelhofen, P. M., P. Gies, C. Roy, and W. J. Randel. 1999. Surface UV radiation over Australia, 1979–1992: effects of ozone and cloud cover changes on variations of UV radiation. *Journal of Geophysical Research* **104**:19,135–19,159.
- van de Mortel, T. F., and W. A. Buttemer. 1996. Are *Litoria aurea* eggs more sensitive to ultraviolet-B radiation than eggs of sympatric *L. peronii* or *L. dentata*? *Australian Zoology* **30**:150–157.
- Weygoldt, P. 1989. Changes in the composition of mountain stream frog communities in the Atlantic Mountains of Brazil: frogs as indicators of environmental deteriorations? *Studies of Neotropical Fauna and Environment* **24**:249–255.
- Wilson, L. D., and J. R. McCranie. 1993. Status of amphibian populations in Honduras. Pages 81–82 in J. L. Vial and L. Saylor, editors. *Declining amphibian populations task force (DAPTF) working document no. 1. The status of amphibian populations: a compilation and analysis*. DAPTF report. World Conservation Union/Species Survival Commission, Gland, Switzerland.
- Yan, N. D., W. Keller, N. M. Scully, D. R. S. Lean, and P. J. Dillon. 1996. Increased UV-B penetration in a lake owing to drought-induced acidification. *Nature* **381**:141–143.
- Zaga, A., E. E. Little, C. F. Rabeni, and M. R. Ellersieck. 1998. Photoenhanced toxicity of a carbamate insecticide to early leaf stage amphibians. *Environmental Toxicology and Chemistry* **17**:2022–2035.
- Ziemke, J. R., J. R. Herman, J. L. Stanford, and P. K. Bhartia. 1998. Total ozone/UV-B monitoring and forecasting: impact of clouds and the horizontal resolution of satellite retrievals. *Journal of Geophysical Research* **103**:3865–3871.



Appendix 1

Summary of site descriptions, species loss, and other taxonomic information for 11 Central American survey sites.^a

Site no.	Country	Location	Dominant vegetation	Elevation (m)	Latitude (degrees)	Longitude (degrees)	No. of species		Species decline index (SDI) ^c	Declines occurred ^d		Taxa lost or declined				Taxa not declined					
							lost or declined	remaining ^b		after	before	family	no. genera	no. species (100% loss) ^e	family	no. genera	no. species				
s134	Costa Rica	Lower Penas Blancas Valley, Monteverde	montane/ cloud forest	850	10.30	-84.77	30	0	30.00	Dec 86	Jan 88	Bufonidae	2	4(3)	none						
												Centrolenidae	2	3(1)							
												Hylidae	5	9(5)							
												Leptodactylidae	2	13(7)							
												Ranidae	1	1(1)							
s132	Costa Rica	upper slopes, Monteverde	montane/ cloud forest	1450	10.32	-84.80	27	1	26.04	Dec 86	Jan 88	Bufonidae	2	2(2)	Bufonidae	1	1				
												Centrolenidae	2	3(1)							
												Hylidae	3	7(5)							
												Leptodactylidae	1	10(2)							
												Microhylidae	1	1(1)							
												Plethodontidae	1	2(0)							
												Ranidae	1	2(2)							
s133	Costa Rica	Upper Penas Blancas Valley, Monteverde	montane/ cloud forest	1250	10.30	-84.78	26	0	26.00	Dec 86	Jan 88	Bufonidae	2	2(1)	none						
												Centrolenidae	2	3(1)							
												Hylidae	4	7(5)							
												Leptodactylidae	1	13(3)							
												Ranidae	1	1(1)							
s131	Costa Rica	Pacific slope, Monteverde	montane/ cloud forest	1275	10.32	-84.82	24	1	23.04	Dec 86	Jan 88	Bufonidae	2	2(1)	Bufonidae	1	1				
												Centrolenidae	2	5(3)							
												Hylidae	3	7(4)							
												Leptodactylidae	1	6(1)							
												Microhylidae	1	1(1)							
												Plethodontidae	1	1(0)							
												Ranidae	1	2(2)							
s102	Panama	Fortuna	montane/ cloud forest	1100	8.73	-82.23	15	0	15.00	Dec 95	Dec 96	Bufonidae	2	2(2)	none						
												Centrolenidae	1	1(0)							
												Dendrobatidae	1	3(3)							
												Hylidae	3	7(5)							
												Leptodactylidae	1	2(2)							

continued

Appendix 1 (continued)

Site no.	Country	Location	Dominant vegetation	Elevation (m)	Latitude (degrees)	Longitude (degrees)	No. of species		Declines occurred ^d		Taxa lost or declined				Taxa not declined		
							lost or declined	remaining ^b	Species decline index (SDI) ^c	after	before	family	no. genera	no. species (100% loss) ^e	family	no. genera	no. species
s101	Costa Rica	Las Tablas	montane/cloud forest	1900	8.92	-82.73	10	0	10.00	Jun 93	Dec 93	Bufonidae	2	2(2)	none		
												Hylidae	1	3(2)			
												Leptodactylidae	1	3(3)			
												Plethodontidae	1	1(1)			
												Ranidae	1	1(1)			
s013	Puerto Rico	El Yunque	montane/cloud forest	660	18.03	-66.50	6	1	≤5.14	uncertain	1982	Leptodactylidae	1	6(3) ^f	Leptodactylidae	1	1 ^b
s004	Honduras	Parque Nacional Cusco	not available	750	15.52	-88.20	4	0	≤4.00	uncertain	Dec 92	Hylidae	2	3(3)			not available ^b
												Leptodactylidae	1	1(1)			
s103	Costa Rica	Jardin Botánico Wilson	montane/cloud forest	1100	8.13	-83.37	2	0	≤2.00	Dec 86	Jul 90	Bufonidae	1	1(1)			not available ^b
s104	Panama	Cerro Pando (east)	montane/cloud forest	1800	8.92	-82.75	1	0	≤1.00	Jan 94	Dec 97	Dendrobatidae	1	1(1)			not available ^b
s105	Panama	Las Nubes	montane/cloud forest	1800	8.77	-82.92	1	0	≤1.00	Jan 94	Dec 97	Bufonidae	1	1(1)			not available ^b

^aThis information was synthesized from an unpublished database compiled by the Declining Amphibian Populations Task Force (Carey et al. 2001).

^bThere may be additional taxa that did not decline but that were not considered or recorded in the survey for this study.

^cSDI = (number of amphibian species exhibiting severe or total population declines ÷ total number of amphibian species present).

^dAfter refers to the date after which declines occurred following a field survey when conditions appeared normal. Before refers to the first date of a field site survey following a die-off event. Where possible, both the month and the year are reported; otherwise, only the year is reported.

^ePopulation loss is approximately 75% for the other species that experienced severe population declines.

^fPopulation loss is approximately 25% for the other species that experienced moderate population declines.

Appendix 2

Summary of the site descriptions, species loss, and other taxonomic information for the nine South American survey sites.^a

Site no.	Country	Location	Dominant vegetation	Elevation (m)	Latitude (degrees)	Longitude (degrees)	No. of species		Species decline index (SDI) ^c	Declines occurred ^d		Taxa lost or declined				Taxa not declined			
							lost or declined	remaining ^b		after	before	family	no. genera	no. species (100% loss) ^e	family	no. genera	no. species		
s113	Brasil	San Teresa, Espirito Santo	montane/ cloud forest	750	-19.92	-30.67	8	3	5.82	1986	Sep 87	Centrolenidae	1	1(1)	Hylidae	2	3		
s017	Venezuela	Cortillera de Merida	not available	4000	8.40	-71.13	5	0	≤5.00	Jun 88	Mar 90	Dendrobatidae	1	1(0)					
												Hylidae	1	1(1)					
s111	Brasil	Boracéia, São Paulo	montane/ cloud forest	850	-23.63	-45.83	11	16	4.48	Mar 79	1982	Leptodactylidae	3	5(5)	not available ^b				
s112	Brasil	Teresopolis, Rio de Janeiro	montane/ cloud forest	900	-22.45	-42.98	2	0	≤2.00	1979	1979	Bufonidae	1	1(0)	Bufonidae	2	2		
												Hylidae	1	1(0)	Hylidae	3	11		
s114	Brasil	Itatiaia, Rio de Janeiro	montane/ cloud forest	1650	-22.38	-44.65	1	0	≤1.00		1982	Leptodactylidae	1	1(1)	Leptodactylidae	2	3		
s115	Brasil	Brejo da Lapa, Minas Gerais	montane/ cloud forest	1900	-22.37	-44.73	1	0	≤1.00	Mar 79	Nov 84	Leptodactylidae	1	1(1)	not available ^b				
s007	Peru	Cuzco Amazonico	evergreen/ semi-evergreen rain forest	200	-12.58	-69.08	0	33	0.00	N/A	N/A	Leptodactylidae	1	1(1)	not available ^b				
s010	Peru	Madre de Dios	monsoon forest	350	-11.85	-71.32	0	81	0.00	N/A	N/A	none			Bufonidae	1	1		
												Dendrobatidae			Hylidae	6	10		
												Leptodactylidae			Leptodactylidae	6	17		
												Pseudidae			Microhylidae	3	3		
												Bufonidae			Bufonidae	1	3		
												Dendrobatidae			Dendrobatidae	3	8		
s029	Brasil	Reserva Florestal Adolpho Ducke, Amazonas	monsoon forest	60	-2.87	-59.98	0	42	0.00	N/A	N/A	Leptodactylidae			Hylidae	9	37		
												Leptodactylidae			Leptodactylidae	10	29		
												Microhylidae			Microhylidae	4	4		
												Bufonidae			Bufonidae	2	4		
												Centrolenidae			Centrolenidae	1	1		
												Dendrobatidae			Dendrobatidae	3	3		
s010	Peru	Madre de Dios	monsoon forest	350	-11.85	-71.32	0	81	0.00	N/A	N/A	none			Hylidae	5	17		
												Leptodactylidae			Leptodactylidae	4	13		
												Microhylidae			Microhylidae	2	3		
												Pipidae			Pipidae	1	1		

^aThis information was synthesized from an unpublished database compiled by the Declining Amphibian Populations Task Force (Carey et al. 2001). There may be additional taxa that did not decline but that were not considered or recorded in the survey for this study.

^bSDI = (number of amphibian species exhibiting severe or total population declines) / total number of amphibian species present.

^cAfter refers to the date after which declines occurred following a field survey when conditions appeared normal. Before refers to the first date of a field site survey following a die-off event. Where possible, both the month and the year are reported; otherwise, only the year is reported.

^dPopulation loss is approximately 75% for the other species that experienced severe population declines.