

VARIABLE BREEDING PHENOLOGY AFFECTS THE EXPOSURE OF AMPHIBIAN EMBRYOS TO ULTRAVIOLET RADIATION

PAUL STEPHEN CORN^{1,3} AND ERIN MUTHS²

¹U.S. Geological Survey Northern Rocky Mountain Science Center, Aldo Leopold Wilderness Research Institute, P.O. Box 8089, Missoula, Montana 59807 USA

²U.S. Geological Survey Midcontinent Ecological Science Center, 2150 Centre Avenue, Building C, Fort Collins, Colorado 80526-8118 USA

Abstract. Reduced water depth in dry years has been proposed to interact with ultraviolet-B (UV-B) radiation and a pathogenic fungus to cause episodes of high mortality of amphibian embryos. Observations of breeding phenology of boreal chorus frogs (*Pseudacris maculata*) in Colorado from 1986 to 2001 show that dry years result in earlier breeding. The earliest and latest dates of maximum calling activity by males were 20 May and 16 June, and the date of maximum calling was strongly related to the amount of snow accumulation during the winter. Surface UV-B flux, estimated from satellite-based measurements, was positively related to date of maximum calling. In dry years, surface UV-B during calling was reduced by an amount similar to that attributed to reduced depth. Although there was a significant trend of increasing UV-B from 1978 to 2001 on the average date (2 June) of maximum calling activity, there was no relationship between year and surface UV-B at actual dates of maximum calling. Exposure to extreme temperatures is an alternative explanation for increased mortality of amphibian embryos in shallow water.

Key words: amphibians; boreal chorus frog; breeding phenology; global change; *Pseudacris maculata*; ultraviolet radiation.

INTRODUCTION

Changes in external physical factors have often been invoked as causes for recent declines of amphibian species in several places around the world (Waldman and Tocher 1998, Alford and Richards 1999, Boone et al. 2002). Embryos of several species suffer increased mortality when experimentally exposed to ambient ultraviolet-B radiation (UV-B), and increased UV-B due to thinning stratospheric ozone is hypothesized as a possible cause of amphibian declines (Blaustein et al. 1998). More fundamentally, species that breed in open water require water, and extinctions of cloud forest-dwelling species in Costa Rica are correlated with increased drying during years with strong El Niño Southern Oscillation (ENSO) events (Pounds et al. 1999). Survival of embryos depends on temperatures within a specific range (Moore 1949), and temperature also is an important determinant of the timing of breeding (Reading 1998). Some species of amphibians in Great Britain are breeding significantly earlier in the year in response to warmer spring weather in the last 20 yr (Beebee 1995, Forchhammer et al. 1998), and shifts in phenology may have complex effects on populations, some of which can be negative (Donnelly and Crump 1998).

However, except for obvious habitat destruction, few amphibian declines can be demonstrated to have been

caused by single factors (Corn 2000), and interactions among two or more factors are likely important for declines without apparent causes (Alford and Richards 1999). Changing climates may create conditions in which multiple factors interact to create increased risk (Pounds 2001). In the Pacific Northwest, ENSO events result in low winter precipitation in the Cascade Mountains. In the following spring, boreal toad (*Bufo boreas*) embryos develop in shallower water than in years with high winter precipitation, and suffer greater mortality than in wetter years when embryos develop in deeper water (Kiesecker et al. 2001). At depths <20 cm, infection of toad embryos by the pathogenic fungus *Saprolegnia ferax* was >50%. Embryos of *B. boreas* have been shown to be susceptible to *S. ferax* only in the presence of UV-B radiation (Kiesecker and Blaustein 1995). A more recent experiment exposed toad embryos to ambient sunlight and sunlight with UV-B removed at three depths (Kiesecker et al. 2001). Mortality of embryos exposed to ambient sunlight exceeded mortality of embryos protected from UV-B only in the shallowest treatment (10 cm), resulting in the conclusion that, in ENSO years, embryos of *B. boreas* develop in shallower water, are exposed to higher doses of UV-B radiation, and consequently suffer catastrophic mortality from infection by *S. ferax* (Kiesecker et al. 2001).

The data from this experiment in Oregon were described to "... identify a complete chain of events whereby climate change causes wholesale mortality in an amphibian population" (Pounds 2001). However, episodic embryo mortality has not resulted in declines

Manuscript received 5 December 2001; revised 15 June 2002; accepted 19 June 2002.

³ E-mail: scorn@usgs.gov



PLATE 1. (Left) Lily Pond, Larimer County, Colorado, at sunset on 4 June 1988. Snowmelt was in progress, and boreal chorus frogs (*Pseudacris maculata*) were beginning to call from the emergent vegetation. (Right) Boreal chorus frog from Lily Pond. Photographs by P. S. Corn.

of populations of *B. boreas* in Oregon (Olson 2001), and exposure to UV-B is controlled by factors other than water depth alone. Penetration of UV-B in surface water depends on the amount and type of dissolved organic carbon (DOC) (Morris et al. 1995), which are also related to precipitation (Schindler and Curtis 1997). DOC concentration also varies considerably among amphibian breeding habitats (Adams et al. 2001, Peterson et al. 2002, Palen et al. 2002). UV-B flux varies annually and seasonally, and, combined with annual variation in the timing of breeding, results in considerable uncertainty in the amount of UV-B to which amphibian embryos may be exposed.

Ultraviolet radiation incident on the Earth's surface can be estimated using measurements of ozone thickness, cloud transmittance, aerosol amounts, and surface reflectivity by satellite-based total ozone mapping spectrometers (TOMS) (Eck et al. 1995, Udelhofen et al. 1999, Middleton et al. 2001). In this study, we estimated the variation in UV-B flux that can be attributed to variation in the timing of breeding. We used 16 yr of observations of boreal chorus frogs, *Pseudacris maculata* (see Plate 1), at a pond in the mountains of Colorado to document variation in breeding phenology, and we combined these data with satellite-based estimates of UV-B to determine the surface UV-B exposure during breeding.

METHODS

We used observations of calling activity by male *P. maculata* from 1986 to 2001 at Lily Pond, a shallow, snowmelt-filled, vernal pond in the mountains of northern Colorado at an elevation of 2900 m (Vertucci and Corn 1996; see Plate 1), to quantify annual variation in breeding phenology. Breeding activity was defined by the date of maximum calling activity, estimated by two methods. From 1994 to 2000, we quantified calling intensity from tape recordings made by an automated recording system (Corn et al. 2000). One 12–18 s re-

ording was made each hour, and calling intensity was scored on a scale of 0 (none) to 3 (multiple, overlapping calls). A call saturation index (CSI) was computed for each day by summing the scores and dividing by 72 (the number of observations, 24, times 3, the maximum possible score). The middle day of the 3-d period with the highest mean CSI was defined as the day of maximum calling activity. Before 1994 and in 2001 (equipment failure), we interpolated the date when the maximum numbers of males were present in the breeding chorus based on capture–recapture efforts.

To investigate environmental influences on breeding phenology, we used snow accumulation (measured as the water equivalent) and mean daily temperature collected by an automated SNOTEL designated Joe Wright, 5 km southwest of Lily Pond. The SNOTEL (SNOWpack TELEmetry) network is operated by the Natural Resources Conservation Service, and data were obtained from the National Water and Climate Center.⁴

We obtained UV-B exposure data for 19 yr from the Nimbus-7 (1986–1992) and Earth Probe (1997–2001) missions (data were obtained from the National Aeronautics and Space Administration).⁵ Daily estimates of UV, adjusted for terrain height, agree well with ground-based measurements when summed over a week or more (Herman et al. 1996, 1999, Udelhofen et al. 1999). Due to satellite failure, no TOMS data are available for 1993–1996. Data are provided as erythemal exposure (UV-B weighted by the action spectrum for human skin irritation) and represent an estimate for a pixel of 1° latitude by 1.25° longitude, adjusted by the average elevation of the pixel. The TOMS data likely underestimate the exposure at Lily Pond at 2900 m. However, the patterns of variation are the most important aspect of these data, and we do not compare UV-B at Lily Pond to anywhere else. Therefore, we

⁴ URL: <http://www.wcc.nrcs.usda.gov/>

⁵ URL: <http://jwocky.gsfc.nasa.gov/index.html>

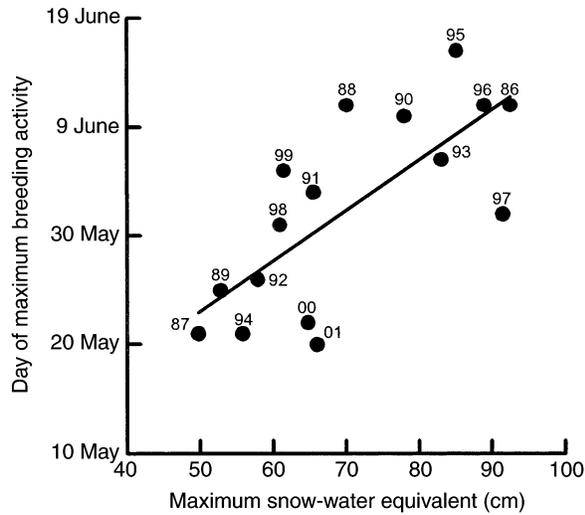


FIG. 1. Relationship between calling activity by male *P. maculata* and maximum snow accumulation (snow-water equivalent, cm) at Lily Pond, Colorado, USA. Data are labeled by year of observation.

have not recalculated the erythemal exposures to account for the specific elevation at Lily Pond.

We used data from the pixel centered at 40.5° N, 105.625° W. In each year for each day from 1 May to 30 June, we calculated 10-d sums (in kJ/m²) of the daily erythemal exposure (J/m²). For example, the 10-d sum for 1 May 1986 was the sum of daily values from 27 April to 5 May 1986, divided by 10³. We used 10 d so that the satellite estimates would more accurately reflect surface irradiance, and because 10 d typically encompasses embryogenesis in *P. maculata*.

RESULTS

Calling by male *P. maculata* at Lily Pond varied considerably from year to year. The earliest date of maximum calling was 20 May, and the latest was 16

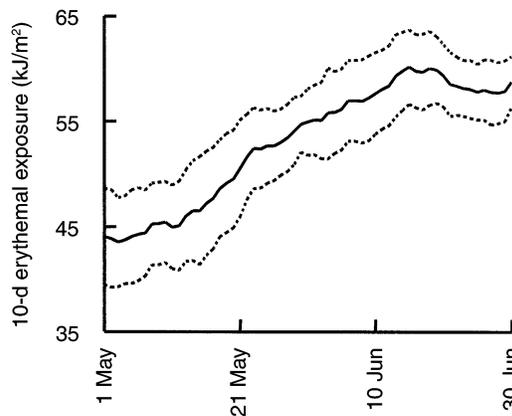


FIG. 2. Mean 10-d TOMS estimates of UV-B (solid line, $n = 19$ yr: 1979–1992 and 1997–2001) in northern Colorado from 1 May to 30 June. Dashed lines indicate upper and lower 95% confidence intervals.

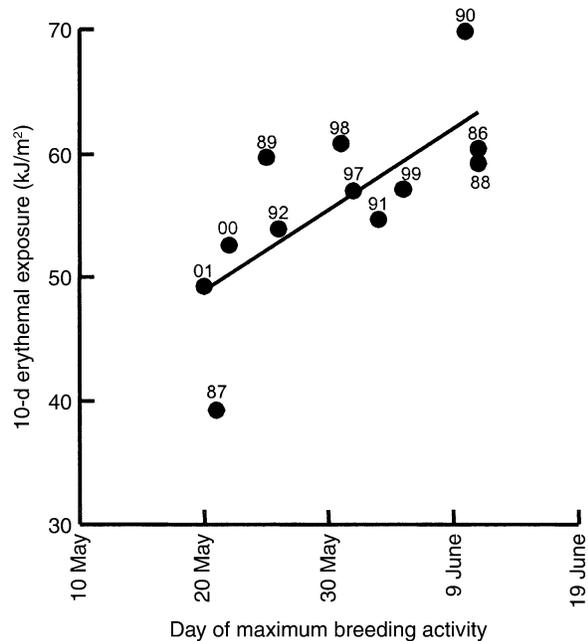


FIG. 3. Estimated 10-d sum of surface UV-B during maximum calling activity by *P. maculata* at Lily Pond. Data are labeled by year of observation.

June. There was no relationship between date of maximum calling and year (linear regression: $F = 0.83$, $P = 0.38$). Neither was there a significant relationship between date of maximum calling and mean temperature from 1 April to 15 May ($F = 1.83$, $P = 0.21$). Timing of calling, however, was strongly dependent on maximum snow accumulation (Fig. 1; $Y = 0.463X + 119.9$, $r^2 = 0.54$, $P = 0.001$).

Changes in the date of maximum calling resulted in changes in surface UV-B exposure. UV-B flux in-

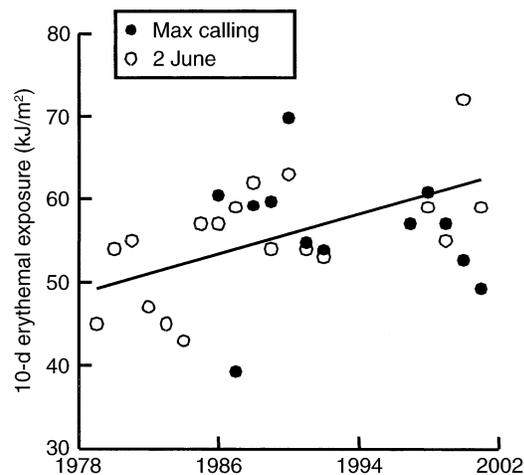


FIG. 4. Estimated 10-d sums of surface UV-B on 2 June, the average date of maximum calling activity by *P. maculata* at Lily Pond (open circles, regression line) and on the actual dates of maximum calling activity (solid circles).

creased during the spring (Fig. 2), which resulted in frogs that bred in May being exposed to less UV-B than frogs that bred in June. The average 10-d UV-B on 16 June (the latest day of maximum calling activity) was 59.7 kJ/m², and average 10-d UV-B on 20 May (the earliest day of maximum calling activity) was 49.5 kJ/m², a decrease of 17%. Using estimated UV-B for individual years, the minimum estimated 10-d UV-B, 39.2 kJ/m² in 1987 (21 May), is a 44% reduction from the maximum 10-d UV-B, 69.8 kJ/m² in 1990 (10 June). The regression of UV-B on day of maximum calling activity also showed a significant decrease in UV-B when breeding occurred earlier (Fig. 3; $Y = 0.656X - 42.97$, $r^2 = 0.53$, $P = 0.007$).

The TOMS data suggest that UV-B during the spring has increased in Colorado during the past two decades. There was a significant increase in the estimated surface UV-B on 2 June, the average date of maximum calling by *P. maculata* at Lily Pond, between 1979 and 2001 (Fig. 4; $Y = 0.597X - 1132.4$, $r^2 = 0.37$, $P = 0.006$). However, using estimated UV-B for individual years, there was no relationship between year and the surface UV-B estimated for each year during breeding (Fig. 4; $F = 0.09$, $P = 0.78$).

DISCUSSION

In snow-dominated landscapes, such as the mountains of western North America, phenology of many organisms, including amphibians, is determined by the timing of snow melt (Inouye et al. 2000, Corn, *in press*). Our results suggest that, despite a recent trend of increasing UV-B in Colorado during the time when amphibians are breeding, embryos of *P. maculata* have not been exposed to an increase in UV-B, because of variation in the timing of breeding. Breeding occurs earlier in the spring in dry years and UV-B flux increases during spring, therefore, frogs may be exposed to less UV-B in dry years. Our data show that this decrease can be of similar magnitude as increases in UV-B due to shallower depths in dry years. For example, we observed a 44% decrease in the estimated UV-B exposure between the earliest and latest dates of breeding. In an experiment in Oregon, the same 44% decrease in UV-B resulted from a 40-cm increase in water depth, and survival of *B. boreas* embryos increased to >75% from <50% (Kiesecker et al. 2001). This equivalence is almost certainly coincidental, but it illustrates the opposing effects of earlier breeding vs. lower water levels. Observations of embryos developing in shallower water in dry years are insufficient information to conclude that UV-B dose is higher in dry years.

It is important to note that UV-B estimates do not represent the dose of radiation received by amphibian embryos. Dose is some fraction of surface UV-B, and differences in dose in the same system should be highly correlated with surface UV-B. Daily TOMS estimates of UV-B can also vary significantly from ground-based

measurements, but accuracy is increased when estimates are integrated over several days (Herman et al. 1999). The estimates of UV-B should be used cautiously, but they are also the only estimates available for comparing to our long-term observations of *P. maculata*.

Determining the actual dose received by aquatic stages of amphibians is complex, and depends not only on radiation incident to the surface, but also on water chemistry, location of egg masses, structure of terrestrial and aquatic vegetation (shading), and other factors. No study yet has measured the UV-B dose on amphibians in the field. However, Diamond et al. (2002) compared the dose-response relationships of three species of *Rana* to estimated UV-B exposure in 26 wetlands and found that 21 sites never received the level of UV-B exposure that caused mortality or malformations in controlled experiments. Two other recent studies have attempted to characterize spatial variation in UV-B exposure in amphibian habitats. Palen et al. (2002) used attenuation coefficients from 136 ponds in the U.S. Pacific Northwest to estimate UV-B exposure at 10 cm below the surface. They found that 85% of ponds would not be expected to experience the amount of UV-B associated with mortality of *B. boreas* embryos (Kiesecker et al. 2001). Peterson et al. (2002) found that 99% of surface UV-B was attenuated between 5 and 20 cm depth in 30 wetlands in northern Wisconsin and Minnesota.

Another caveat to our analysis is that we used an index (calling by males), rather than presence and abundance of eggs, to indicate breeding by *P. maculata*. Females of this species deposit their clutch in several small egg masses, which are difficult to detect at Lily Pond because of dense vegetation. Based on observations of other populations of *Pseudacris*, however, we have no reason to suspect that egg deposition is not coincident with calling by males. We also focused on exposure to embryos, rather than other life stages (tadpoles, metamorphosing frogs), but embryos are the only stage that undergoes a static exposure to UV-B. Amphibian larvae may actively avoid exposure to high UV-B (Nagl and Hofer 1997, van de Mortel and Buttemer 1998).

Seasonal and spatial variation may raise questions about increased exposure to UV-B as a cause of amphibian declines, but are there other consequences to variation in the timing of breeding? Extreme temperatures can be lethal to amphibian embryos, and temperature stress is as plausible a hypothesis as increased UV-B to explain episodes of high mortality of *B. boreas* observed in Oregon (Blaustein et al. 1994, Kiesecker et al. 2001). Mean temperatures did not differ among the treatments at different depths in the Oregon experiment, but temperature ranges were not reported (Kiesecker et al. 2001). The extremes of temperature are likely more important than the mean, and temperature is more variable in shallower water. Data from

an amphibian-breeding site in western Montana show this clearly (P. S. Corn, *unpublished data*). Automated loggers recorded water temperatures hourly during April 2000, when three amphibian species were breeding. One logger (littoral) was placed next to the bank, resting on the bottom in water 5 cm deep, and the other logger (deep) was suspended 10 cm below the surface in water 50 cm deep. Mean temperatures were similar for both locations (littoral = 9.9°C, deep = 9.3°C), but the minimum temperature was lower at the littoral location (2.1°C vs. 4.2°C). The range of temperatures at the littoral location (20.9°C) was twice the range at the deep location (10.4°C). An experiment on *B. boreas* embryos at two sites (Kettle Tarn and Lost Lake) in Colorado found no mortality due to UV-B, but did observe significant mortality between sites that may have been related to temperature (Corn 1998). At Kettle Tarn, embryos were reared at a mean depth of 9.8 cm, and water temperature varied between 6° and 19°C. Embryo mortality at this site was 28%. At Lost Lake, embryos were reared at 3.4 cm, and water temperature varied from 0.5° to 23.6°C. Embryo mortality was 42%. The experiment was not designed to test the effects of temperature on embryo mortality. Therefore, it is unknown whether the more extreme temperatures were responsible for the higher mortality at Lost Lake. However, the differences in mortality are similar to those attributed to UV-B for embryos reared at different depths (Kiesecker et al. 2001).

In central Colorado, there is a trend toward later dates of the last killing frost, but the timing of snow melt has not changed (Inouye et al. 2000). This increases the risk of exposure to lethal temperatures to organisms, such as amphibians, whose phenology is controlled by snow melt. Extreme temperatures, which have been largely ignored in discussions of amphibian decline, are likely to become increasingly important, if scenarios of future climate change prove correct (McCarty 2001). Ultimately, whether temperature or UV-B is the greater proximate risk factor resulting from climate change, much of the variation introduced by climate change is unlikely to be beneficial to amphibian populations (Ovaska 1997, Donnelly and Crump 1998).

ACKNOWLEDGMENTS

We thank J. Herman and E. Weatherhead for advice and assistance with the UV-B data. M. Adams, P. Brooks, B. Bury, W. Palen, two anonymous reviewers, and the Associate Editor, B. Sinervo, provided comments that greatly improved the manuscript. Fieldwork from 1986 to 1992 was supported by the U.S. Fish and Wildlife Service National Acid Precipitation Assessment Program and Global Change Research Program. Fieldwork from 1993 to 1995 was supported by the National Biological Service Global Change Research Program, and fieldwork from 1996 to 2001 was supported by the U.S. Geological Survey Global Change Research Program and Amphibian Research and Monitoring Initiative.

LITERATURE CITED

- Adams, M. J., D. E. Schindler, and R. B. Bury. 2001. Association of amphibians with attenuation of ultraviolet-B radiation in montane ponds. *Oecologia* **128**:519–525.

- Alford, R. A., and S. J. Richards. 1999. Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics* **30**:133–165.
- Beebee, T. J. C. 1995. Amphibian breeding and climate. *Nature* **374**:219–220.
- Blaustein, A. R., D. G. Hokit, R. K. O'Hara, and R. A. Holt. 1994. Pathogenic fungus contributes to amphibian losses in the Pacific Northwest. *Biological Conservation* **67**:251–254.
- 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.
- Boone, M. D., P. S. Corn, M. A. Donnelly, E. E. Little, and P. H. Niewiarowski. 2002. Physical stressors. In G. Linder, C. A. Bishop, and D. A. Sparling, editors. *Global decline of amphibian populations: an integrated analysis of multiple stressor effects*. Society of Environmental Toxicology and Chemistry, Pensacola, Florida, USA, *in press*.
- Corn, P. S. 1998. Effects of ultraviolet radiation on boreal toads in Colorado. *Ecological Applications* **8**:18–26.
- Corn, P. S. 2000. Amphibian declines: review of some current hypotheses. Pages 663–696 in D. W. Sparling, C. A. Bishop, and G. Linder, editors. *Ecotoxicology of amphibians and reptiles*. SETAC Press, Pensacola, Florida, USA.
- Corn, P. S. *In press*. Amphibian breeding and climate change: the importance of snow in the mountains. *Conservation Biology*.
- Corn, P. S., E. Muths, and W. M. Iko. 2000. A comparison in Colorado of three methods to monitor breeding amphibians. *Northwestern Naturalist* **81**:22–30.
- Diamond, S. A., G. S. Peterson, J. E. Tietge, and G. T. Ankley. 2002. Assessment of the risk of solar ultraviolet radiation to amphibians. III. Prediction of impacts in selected northern mid-western wetlands. *Environmental Science and Technology* **36**:2866–2874.
- Donnelly, M. A., and M. L. Crump. 1998. Potential effects of climate change on two neotropical amphibian assemblages. *Climatic Change* **39**:541–561.
- Eck, T. F., P. K. Bhartia, and J. B. Kerr. 1995. Satellite estimation of spectral UVB irradiance using TOMS derived total ozone and UV reflectivity. *Geophysical Research Letters* **22**:611–614.
- Forchhammer, M. C., E. Post, and N. C. Stenseth. 1998. Breeding phenology and climate. *Nature* **391**:29–30.
- 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, Atmospheres* **104**:12059–12076.
- Inouye, D. W., B. Barr, K. B. Armitage, and B. D. Inouye. 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences (USA)* **97**:1630–1633.
- Kiesecker, J. M., and A. R. Blaustein. 1995. Synergism between UV-B radiation and a pathogen magnifies amphibian embryo mortality in nature. *Proceedings of the National Academy of Sciences (USA)* **92**:11049–11052.
- Kiesecker, J. M., A. R. Blaustein, and L. K. Belden. 2001. Complex causes of amphibian population declines. *Nature* **410**:681–684.
- McCarty, J. P. 2001. Ecological consequences of recent climate change. *Conservation Biology* **15**:320–331.
- Middleton, E. M., J. R. Herman, E. A. Celarier, J. W. Wilkinson, C. Carey, and R. J. Rusin. 2001. Evaluating ultraviolet radiation exposure with satellite data at sites of am-

- phibian declines in Central and South America. *Conservation Biology* **15**:914–929.
- Moore, J. A. 1949. Geographic variation of adaptive characters in *Rana pipiens* Schreber. *Evolution* **3**:1–24.
- Morris, D. P., H. Zagarese, C. E. Williamson, E. G. Balseiro, B. R. Hargreaves, B. Modenutti, R. Moeller, and C. Queimados. 1995. The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnology and Oceanography* **40**:1381–1391.
- 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.
- Olson, D. H. 2001. Ecology and management of montane amphibians of the U.S. Pacific Northwest. *Biota* **2**:51–74.
- Ovaska, K. 1997. The vulnerability of amphibians in Canada to global warming and increased solar ultraviolet radiation. Pages 206–225 in D. M. Green, editor. *Amphibians in decline: Canadian studies of a global problem*. Herpetological Conservation 1, Society for the Study of Amphibians and Reptiles, St. Louis, Missouri, USA.
- Palen, W. J., D. E. Schindler, M. J. Adams, C. A. Pearl, R. B. Bury, and S. A. Diamond. 2002. Optical characteristics of natural waters protect amphibians from UV-B in the U.S. Pacific Northwest. *Ecology* **83**:2951–2957.
- Peterson, G. S., L. B. Johnson, R. P. Axler, and S. A. Diamond. 2002. Assessment of the risk of solar ultraviolet radiation to amphibians. II. In situ characterization of exposure in amphibian habitats. *Environmental Science and Technology* **36**:2859–2865.
- Pounds, J. A. 2001. Climate and amphibian declines. *Nature* **410**:639–640.
- 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.
- Reading, C. J. 1998. The effect of winter temperatures on the timing of breeding activity in the common toad *Bufo bufo*. *Oecologia* **117**:469–475.
- 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**:1–8.
- 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, Atmospheres* **104**:19135–19159.
- van de Mortel, T. F., and W. A. Buttemer. 1998. Avoidance of ultraviolet-B radiation in frogs and tadpoles of the species *Litoria aurea* and *L. peronii*. *Proceedings of the Linnæan Society of New South Wales* **119**:173–179.
- Vertucci, F. A., and P. S. Corn. 1996. Evaluation of episodic acidification and amphibian declines in the Rocky Mountains. *Ecological Applications* **6**:449–457.
- Waldman, B., and M. Tocher. 1998. Behavioral ecology, genetic diversity, and declining amphibian populations. Pages 395–443 in T. Caro, editor. *Behavioral ecology and conservation biology*. Oxford University Press, New York, New York, USA.