Ethology **106**, 921—931 (2000)

ISSN 0179–1613

Department of Zoology, Oregon State University, Oregon

Effects of UV-B Radiation on Anti-predator Behavior in Three Species of Amphibians

Lee B. Kats, Joseph M. Kiesecker, Douglas P. Chivers & Andrew R. Blaustein

Kats, L. B., Kiesecker, J. M., Chivers, D. P. & Blaustein, A. R. 2000: Effects of UV-B radiation on anti-predator behavior in three species of amphibians. Ethology **106**, 921—931.

Abstract

Ultraviolet radiation has been suggested as a possible contributing cause of amphibian declines around the world. Both laboratory and field studies have demonstrated that exposure to ultraviolet radiation can lead to increased mortality of developing amphibians. Virtually no studies have examined the sub-lethal effects of ultraviolet on amphibian behavior. In this study, we examine the anti-predator behavior of three species of amphibians after short-term exposure to ultraviolet-B radiation. Toad (*Bufo boreas*) juveniles that had been exposed to ultraviolet radiation did not respond to chemical extracts from conspecifics and heterospecifics as much as juveniles that had not been exposed. Both newt larvae (*Taricha granulosa*) that had been exposed to ultraviolet radiation and those that had not been exposed responded to chemical cues from conspecific predators by increasing the amount of time spent in shelter. Frog tadpoles (*Rana cascadae*) that had been exposed to ultraviolet radiation did not reduce their movement in response to chemical cues from predators as much as tadpoles that had not been exposed. These results indicate that ultraviolet exposure may have important sub-lethal effects in amphibians that could adversely effect their fitness.

Corresponding author: L. B. Kats, Natural Science Division, Pepperdine University, Malibu, CA, 90263, USA. E-mail: lee.kats@pepperdine.edu

Introduction

The effects of ultraviolet (UV) radiation on amphibians have received a great deal of attention, in part because of the possible contribution of UV-B to amphibian population declines. Whilst there are a variety of possible causes for amphibian declines, recent experimental evidence has indicated that ambient levels of UV-B can cause amphibian embryo and larval mortality (Blaustein et al. 1994;

U. S. Copyright Clearance Center Code Statement: 0179-1613/2000/10610–0921$15.00/0

Kiesecker & Blaustein 1995; Anzalone et al. 1998; Blaustein et al. 1998). Despite increasing attention on the effects of UV-B on amphibians, there have been virtually no studies that have examined sub-lethal effects of UV-B on amphibians. If some species of amphibian larvae are susceptible to lethal effects from UV-B radiation, we suggest that amphibians may also incur sub-lethal effects that could be more difficult to detect.

Few studies have examined the sub-lethal effects of UV on behavior. The behavior of a unicellular flagellate, *Euglena gracilis*, is known to be effected by UV-B (Häder 1986). After 2 h of ambient exposure to UV-B, *Euglena* had reduced motility and had drastically impaired phototactic orientation. In another study, mice (*Mus musculus*) that were irradiated for several months with UV-A showed a variety of behavioral abnormalities and had significantly reduced learning ability (Hiramoto et al. 1996). Despite growing numbers of studies examining the effects of UV on amphibian mortality, only one study has reported the effects of UV exposure on amphibian behavior (Nagl & Hofer 1997). They noted that Alpine newt larvae (*Triturus alpestris*) swam erratically when exposed to UV-B radiation.

The purpose of our study was to examine the effects of short-term UV-B exposure on the responses of amphibians to apparent predation risk. Many amphibians have a variety of anti-predator behaviors, such as avoiding risky microhabitats, taking refuge and reducing movement. Many of these behaviors are mediated via chemical cues from the predator (reviewed in Kats & Dill 1998) or via chemical alarm signals (reviewed in Chivers & Smith 1998). In the current study, we examined the behavioral responses of three species of amphibians to predator chemical cues or alarm cues after short-term exposure to UV-B. Previous studies had indicated that *Bufo boreas* metamorphs avoid conspecific alarm cues (Chivers et al. 1999); newt (*Taricha*) larvae increase refuge use in response to odors of adult conspecifics (Elliott et al. 1993) and *Rana cascadae* tadpoles reduce movement in response to predatory newts (Hokit & Blaustein 1995). If UV radiation exposure impacts amphibian locomotion or orientation, as it has been demonstrated for other organisms, we predict that UV-B could have significant sub-lethal effects on amphibian anti-predator behavior.

Methods

Effects of UV-B Radiation on Alarm Responses of Juvenile Toads

To examine the effects of UV-B exposure on alarm reactions, we tested the avoidance response of individual juvenile toads (*Bufo boreas*) to two different stimuli: (i) chemical stimuli from injured conspecifics; and (ii) chemical stimuli from injured heterospecifics. We collected toad metamorphs from Lost Lake (Linn Co., Oregon, 97 km east of Albany, Oregon, elevation 1220 m). Toads were individually placed into 850-ml plastic cups, each of which was lined with moist filter paper. Toads were maintained on a 14 h light : 10 h dark illumination regime at approximately 16 °C and were fed small crickets *ad libitum*. All toads were housed under UV generating lights (Q-Panel UVB313 lamps; Hays et al. 1996) for 5 d. Most UV radiation of biological concern is in the 280–315 nm (UV-B) band (Tevini 1993;

Blaustein et al. 1994). To remove UV-C (and a small amount of UV-B), 50 cups, each containing a single toad, were covered with 3-mm glass (cut-off at about 295 nm; UV-B exposed treatment); 50 control toads were covered with 12-mm glass (cut-off at about 320 nm; UV-B blocked treatment). UV-B and UV-A intensities under glass shields were much less than mid-day solar intensities at 45°N latitude at field conditions (Hays et al. 1996; Fig. 1). Nine toads held in control conditions (UV-B blocked) and one toad exposed to UV-B died during the 5 d in the holding cups. At the conclusion of the 5 d of UV-B exposure, toads were removed from the UV-B treatment and we examined their responses to alarm cues.

To create the chemical alarm cues we euthanized 10 *B. boreas* by decapitation, and a total of 2.15 g of skin tissue was collected and ground using a mortar and pestle. Ground skin tissue was mixed into 230 ml of distilled water and then filtered to obtain an extract which presumably contained chemical alarm cues. The same procedure was used to prepare chemical alarm cues from the heterospecific red-legged frog, *Rana aurora*.

For each trial, we lined the bottom half of a rectangular plastic container (34 × 20 × 9 cm) with a paper towel that was moistened with dechlorinated tap water (control). The bottom of the treatment side of the container was lined with a paper towel that was moistened with 5 ml of either injured conspecific extract or injured heterospecific extract. After the appropriate stimulus was added to each side of the

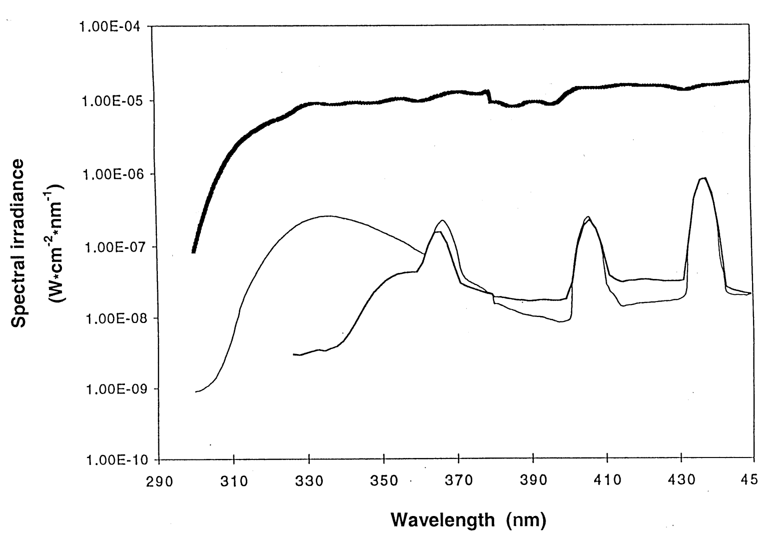

Fig. 1: Spectral of artificial and solar light sources. An International Light IL 1700 spectroradiameter was used to measure the irradiance of the bank of Q-Panel UV-B313 lamps to which experimental animals were subjected. Heavy solid upper line is solar irradiance on a clear day at Corvallis, Oregon (latitude 45°N), 6 Jun. 1996 at solar 13 : 00 h. Light line is irradiance under lamps shielded by 3-mm glass. Lower heavy line is irradiance of lamps shielded by 12-mm glass

test container, we used a spray bottle containing dechlorinated tap water to saturate the paper towels. This ensured that there were no differences in moisture level between the sides. At the start of each trial, we introduced a single *B. boreas* into the center of the container. We recorded which half of the test chamber the toad occupied every 30 min for 2.5 h. To control for the possibility of bias in the toad's orientation in the room, we rotated the containers 180° every half hour. Sample sizes were as follows: toads that had not been exposed to UV-B (control) with heterospecific alarm cue, $n = 20$; control toads with conspecific alarm cue, $n = 21$; toads exposed to UV-B radiation (experimental) with heterospecific alarm cue, $n = 24$; experimental toads with conspecific alarm cue, $n = 25$. We calculated the mean percentage of observations that toads spent away from the extract from injured frogs and toads. We used a two-way ANOVA on arcsine transformed percentages to examine the effects of alarm chemical extract and the effects of UV exposure.

Effect of UV-B Radiation on Anti-predator Response of Larval Newts to Adult Conspecific Predators

Newt (*Taricha torosa*) larvae are known to respond to chemical cues originating from conspecific predators (Elliott et al. 1993). The purpose of this experiment was to examine the effects of UV-B radiation on the anti-predator behavioral responses of newt (*Taricha granulosa*) larvae to chemical cues from conspecific predators. In this experiment we exposed newt larvae to UV-B radiation under conditions similar to those described above for the toad experiment. Newt larvae were collected from the Corvallis Watershed Reservior (Benton Co., Oregon, elevation 183 m) and ranged in size from 1.6 to 2.3 cm snout–vent length. Five newt larvae were placed into each of 14 glass aquaria (50 × 30 × 25 cm; 37 l) and maintained on a 14 h light : 10 h dark illumination regime at approximately 16 °C. The aquaria were filled to a depth of 3 cm with dechlorinated tap water. Previous data had indicated that 3 cm of water filtered out negligible amounts of UV-B radiation (Kiesecker, unpubl. data). Larvae were fed *Tubifex* worms *ad libitum*. Seven aquaria were randomly assigned as control tanks and seven as UV-B exposed tanks. Both control and UV-B exposed tanks were covered with the same glass shields as described for the toad experiment. During the 18-d exposure regime, four larvae in UV-B blocked tanks and 10 larvae in UV-B exposed tanks died. After this UV-B exposure period, the behavior of UV-B exposed newt larvae was compared to the behavior of control larvae in response to conspecific chemical cues.

Plastic chambers (78 × 40 × 14 cm) were filled to a depth of 5 cm with dechlorinated tap water. Leaves collected from the same habitat as the larvae were placed into the chambers such that they covered half of the bottom area of the chamber (leaves were spaced such that their edges were touching, providing a single layer of shelter). Individual newt larvae were placed into the open end of the chambers and their positions in the chamber (in the open or under leaf litter) were recorded every 15 min for 1 h, at the end of which 1.6 l of either dechlorinated tap water or water taken from a tank containing five adult newts (five adults in 20 l of water for a minimum of 12 h) was uniformly poured into the chambers containing the newt larvae. The positions of the newt larvae were recorded every 15 min for the next 2 h. We used a two-way ANOVA on the arcsine transformed percentage increase in shelter use (% shelter use during cue addition, minus % shelter use before cue addition) to examine the effects of UV exposure and conspecific chemical cues.

Effects of UV-B Radiation on Anti-predator Responses of Tadpoles to Predatory Newts

Adult newts (*T. granulosa*) feed on *Rana cascadae* tadpoles (Peterson & Blaustein 1991). Tadpoles were collected from Three Creeks Lake Area (Deschutes Co., Oregon, 43 km west of Bend, Oregon, elevation 2000 m; Gosner stages 25–35). Six tadpoles were placed into each of 14 different 37-l glass aquaria. The aquaria were filled to a depth of 3 cm with dechlorinated tap water. Seven of the aquaria were randomly assigned as controls (no UV-B) and seven as UV-B exposed, using the same methods as those described above. After 18 d under these conditions, we quantified the anti-predator behavior of tadpoles from both groups towards caged predatory adult newts (*T. granulosa*). During the 18 d of exposure, 10 larvae died from unknown causes in both the control tanks and the UV-B exposed tanks.

Adult newts were collected from Corvallis Watershed Reservoir (see larval newt experiment above) and were held in captivity for a minimum of 3 days. During captivity adult newts were fed mealworms.

To examine the responses of tadpoles to predatory newts, we filled a plastic chamber ($78 \times 40 \times 14$ cm) to a depth of 5 cm with dechlorinated tap water. Two smaller chambers ($9 \times 9 \times 5$ cm), constructed of wooden framing and black nylon screening, were placed at both ends of the larger chamber. One adult newt was placed into one of the end chambers 5 min before the start of an experimental trial and the other chamber remained empty. Either three control tadpoles or three UV-B exposed tadpoles were then placed into a center chamber ($16 \times 12 \times 14$ cm). After 1 min this chamber was lifted and the tadpoles were allowed to swim freely; tadpole behavior was recorded for 5 min. We kept a running total of time during which at least one of the three tadpoles was moving through this chamber. In addition, every 30 s throughout the 5-min trial, we recorded the number of tadpoles (out of three) that were on the half of the chamber opposite the adult newt. We conducted nine replicate experiments with UV-B exposed tadpoles and 10 replicates with control tadpoles. We used the t-test to compare the arcsine transformed percentage of observations that tadpoles were on the side opposite the adult newt. We also used the test to compare the arcsine transformed percentage of time out of 5 min that at least one of three tadpoles was moving.

Results

Effects of UV-B Radiation on Alarm Responses of Juvenile Toads

Toad metamorphs that had been exposed to UV-B did not avoid chemical extracts from conspecifics and heterospecifics as much as metamorphs that had not been exposed to UV-B ($F_{1,86} = 4.67$, $p = 0.033$; Fig. 2). In general, metamorphs avoided alarm cues from injured conspecific toads more strongly than they avoided cues from injured *Rana* ($F_{1,86} = 11.84$, $p = 0.0009$). There was no significant interaction between exposure to UV-B and alarm cues ($F_{1,86} = 0.066$, $p = 0.79$; Fig. 2). There were no visible physical differences between metamorphs that had been exposed to UV-B and those that were not exposed.

Effect of UV-B Radiation on Anti-predator Response of Larval Newts to Adult Conspecific Predators

Both larvae that had been exposed to UV-B and those that had not been exposed significantly increased their shelter use in response to chemical cues from conspecific predators ($F_{1,41} = 42.89$, $p < 0.0001$; Fig. 3). Newt larvae that had been exposed to UV-B did not respond to cues from conspecific predators as much as larvae that had not been exposed; however, the difference was not significant ($F_{1,41} = 2.61$, $p = 0.11$). There was no significant interaction between exposure to UV-B and response to conspecific chemical cues ($F_{1,41} = 0.76$, $p = 0.38$). There were no visible physical differences in larvae that had been exposed to UV-B and those that had not, and all larvae were still living 7 d after the behavior experiment.

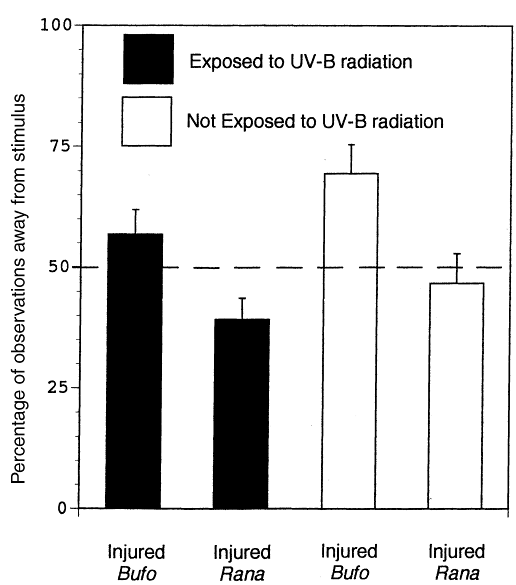

Fig. 2: Mean (± SE) percentage of observations that toad metamorphs (*Bufo boreas*) spent away from chemical stimuli from either injured conspecific or injured *Rana aurora*

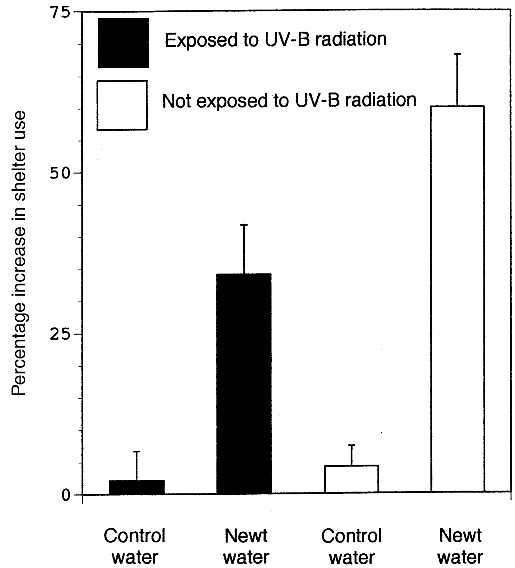

Fig. 3: Mean (± SE) percentage change in shelter use for newt (*Taricha granulosa*) larvae before and after odors from predatory adult conspecifics were added

Effects of UV-B Radiation on Anti-predator Responses of Tadpole Larvae to Predatory Newts

Rana tadpoles that had been exposed to UV-B spent less time avoiding the end of the chamber containing the predatory newt, but the difference was not significant (t-test on arcsine transformed percentage of time away from adult newt: $t = 1.62$, $df = 17$, $p = 0.12$; Fig. 4). However, tadpoles that had been exposed to UV-B spent significantly more time moving than tadpoles that had not been exposed to UV-B (t-test on arcsine transformed percentage time moving: $t = 2.41$, $df = 17$, $p = 0.03$). There were no visible physical differences in tadpoles that had been exposed to UV-B and those that had not been exposed, and all tadpoles were alive 7 d after the behavior experiment.

Discussion

Previous studies have demonstrated that exposure to UV-B radiation causes increased mortality in amphibian embryos (e.g. Worrest & Kimeldorf 1976; Blaustein et al. 1994, 1998) and larvae (e.g. Nagl & Hofer 1997; Ovaska et al. 1997). Virtually no studies have demonstrated more subtle sub-lethal effects of UV-B on amphibian behavior. Our results indicate that short-term exposure to UV-B effects the anti-predator behavior of some amphibians. Both *Bufo* metamorphs and *Rana*

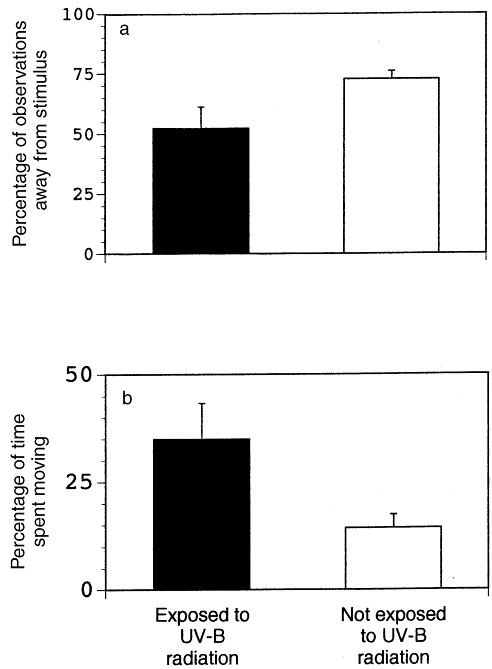

Fig. 4: Mean (± SE) percentage of observations *Rana cascadae* tadpoles spent away from a caged predator (a) and the percentage of time tadpoles moved when in the presence of a caged predator (b), both when exposed and not exposed to UV-B radiation

tadpoles showed reduced anti-predator responses following a period of UV-B exposure. *Taricha* larvae showed a similar, but non-significant, trend toward a reduction in anti-predator behavior. We suggest that relatively short-term exposure to UV-B radiation was potentially stressful to these prey amphibians. In part, changes in behavior of stressed amphibians may be the result of increased levels of circulating corticotropin-releasing hormone. For example, previous studies have demonstrated that elevated corticotropin-releasing hormone in stressed *Taricha granulosa* resulted in increased locomotor activity (Moore et al. 1984; Lowry & Moore 1991). Possible increases in corticotropin-releasing hormone in UV-exposed amphibians might account for the observed decreased refuge behavior of the newt larvae and the increased locomotor activity of *Rana* larvae in response to predator chemical cues in our study.

Amphibians that lose their sensitivity to predators or predator cues because of exposure to UV-B in nature will most likely suffer increased mortality due to predation. Each of the prey that we tested is regularly consumed by predators in the field. Juvenile toads are preyed on by garter snakes (Devito et al. 1998), newt larvae by adult conspecifics (Kerby & Kats 1998), and *Rana* tadpoles by adult newts (Peterson & Blaustein 1991). In the current study, animals exposed to apparent predator risk hid less and moved more than those not exposed. Each of these predator-mediated changes in behavior may increase the vulnerability of larval or juvenile amphibians to predators in nature.

Amphibians are frequently exposed to UV radiation (Blaustein et al. 1998). In addition to effecting anti-predator behavior, exposure to UV-B could effect other behaviors. Free-moving amphibians may be able to detect solar radiation and avoid large doses of UV-B radiation in nature. However, over evolutionary time, certain behaviors may have evolved which expose amphibians to prolonged bouts of UV-B. For example, in the Oregon Cascades, several species lay their eggs in open shallow water, their tadpoles aggregate in open shallow water, and adults may bask in sunlight (Blaustein et al. 1994; Fite et al. 1998). Furthermore, unlike adults, eggs and, under certain conditions, larvae cannot move out of sunlight. Disturbances may exacerbate the effects of UV-B. For example, in southern California, intermittent fires may influence how amphibians lay their eggs and find shelter (Gamradt & Kats 1997; Kerby & Kats 1998). Decreased canopy cover due to fire may temporarily subject eggs, larvae and adults to increased doses of ambient UV-B which may hamper egg development, alter behavior and potentially effect local populations (Kerby & Kats 1998). Similarly, clear-cutting in the Pacific Northwest has drastically decreased forest canopy cover (Norse 1990) where amphibians may find shelter (Walls et al. 1992). Unlike eastern forests that have been cut a little at a time over centuries, the northwestern forests have been clear-cut in large tracts, over decades (Ehrlich 1997). Thus, over a relatively short period, amphibians have been subjected to significant loss of habitat from which they can obtain shelter from solar radiation.

In a previous study, we found that UV-B exposure did not impact on the direction of movement of adult newts (*T. granulosa*) returning to sites from which they had been collected; however, it did impact on the speed at which they returned (Blaustein et al., 2000). Future studies should examine whether UV-B exposure effects other behaviors, including those related to foraging, mating or other social interactions. Whilst UV-B radiation may have contributed to the decline of some amphibian species by causing mortality directly to eggs and larvae, further research is needed to determine whether UV-B is indirectly related to amphibian declines by disrupting behaviors critical for survival.

Acknowledgements

We thank NSF (DEB-942333 and IBN-9904012 to A.R.B; ROA Supplement and IBN-07732 to L.B.K.) and the Katherine Bisbee Fund of the Oregon Community Foundation for support. We thank John Hays for the use of the glass shields and spectroradiometer, and for valuable discussion. We also thank Gordon and Anthea Zellaby, Alan Bernard, Edgar Hargraves, R.L. Buckskin and Nathan Woolsey for their help.

Literature Cited

Anzalone, C. R., Kats, L. B. & Gordon, M. S. 1998: Effects of solar UV-B radiation on embryonic development in three species of lower latitude and lower elevation amphibians. Conserv. Biol. **12**, 646—653.

Blaustein, A. R., Chivers, D. P., Kats, L. B. & Kiesecker, J. M. 2000: Effects of ultraviolet radiation on locomotion and orientation in roughskin newts (*Taricha granulosa*). Ethology **106**, 227—234.

Blaustein, A. R., Hoffman, P. D., Hokit, D. G., Kiesecker, J. M., Walls, S. C. & Hays, J. B. 1994: UV-repair and resistance to solar UV-B in amphibian eggs: a link to amphibian declines. Proc. Natl. Acad. Sci. USA **91**, 1791—1795.

Blaustein, A. R., Kiesecker, J. M., Chivers, D. P., Hokit, D. R., Marco, A., Belden, L. K. & Hatch, A. 1998: Effects of ultraviolet radiation on amphibians: field experiments. Am. Zool. **38**, 799—812.

Chivers, D. P., Kiesecker, J. M., Wildy, E. L., Belden, L. K., Kats, L. B. & Blaustein, A. R. 1999: Avoidance response of post-metamorphic anurans to cues of injured conspecifics and predators. J. Herpetol. **33**, 472—476.

Chivers, D. P. & Smith, R. J. F. 1998: Chemical alarm signalling in aquatic predator–prey systems: a review and prospectus. Écoscience **5**, 338—352.

Devito, J., Chivers, D. P., Kiesecker, J. M., Marco, A., Wildy, E. L. & Blaustein, A. R. 1998: The effects of snake predation on metamorphosis of western toads, *Bufo boreas* (Amphibia, Bufonidae). Ethology **104**, 185—193.

Ehrlich, P. R. 1997: A World of Wounds: Ecologists and the Human Dilemma. Ecology Institute, Oldendorf/Luhe, Germany.

Elliott, S. A., Kats, L. B. & Breeding, J. A. 1993: The use of conspecific chemical cues for cannibal avoidance in California newts (*Taricha torosa*). Ethology **95**, 186—192.

Fite, K. V., Blaustein, A. R., Bengston, L. & Hewitt, H. 1998: Evidence of retinal light damage in *Rana cascadae*: a declining amphibian species. Copeia **1998**, 906—914.

Gamradt, S. C. & Kats, L. B. 1997: Impact of wildfire-induced sedimentation on oviposition of stream-breeding California newts, *Taricha torosa*. Oecologia **110**, 546—549.

Häder, D.-P. 1986: Effects of solar and artificial UV irradiation on motility and phototaxis in the flagellate, *Euglena gracilis*. Photochem. Photobiol. **44**, 651—656.

Hays, J. B., Blaustein, A. R., Kiesecker, J. M., Hoffman, P. D., Pandelova, I., Coyle, C. & Richardson, T. 1996: Developmental responses of amphibians to solar and artificial UV-B sources: a comparative study. Photochem. Photobiol. **64**, 449—456.

Hiramoto, K., Okada, T. & Ito, M. 1996: Abnormalitities in behavior, learning ability, and the cholinergic system induced by long-term ultraviolet A irradiation of mice. Neuropsychology **33**, 182—185.

Hokit, D. G. & Blaustein, A. R. 1995: Predator avoidance and alarm-response behaviour in kin-discriminating tadpoles (*Rana cascadae*). Ethology **101**, 280—290.

Kats, L. B. & Dill, L. M. 1998: The scent of death: Chemosensory assessment of predation risk by prey animals. Écoscience **5**, 361—394.

Kerby, J. L. & Kats, L. B. 1998: Modified interactions between salamander life stages caused by wildfire-induced sedimentation. Ecology **79**, 740—745.

Kiesecker, J. M. & Blaustein, A. R. 1995: Synergism between UV-radiation and a pathogen magnifies amphibian mortality in nature. Proc. Natl. Acad. Sci. USA **92**, 11 049—11 052.

Lowry, C. A. & Moore, F. L. 1991: Corticotropin-releasing factor (CRF) antagonist suppresses stress-induced locomotor activity in an amphibian. Horm. Behav. **25**, 84—96.

Moore, F. L., Roberts, J. & Bevers, J. 1984: Corticotropin-releasing factor (CRF) stimulates locomotor activity in intact and hypophysectomized newts (Amphibia). J. Exp. Zool. **231**, 331—334.

Nagl, A. M. & Hofer, R. 1997: Effects of ultraviolet radiation on early larval stages of the Alpine newt, *Triturus alpestris*, under natural and laboratory conditions. Oecologia **110**, 514—519.

Norse, E. A. 1990: Ancient Forests of the Pacific Northwest. Island Press, Washington, DC.

Ovaska, K., Davis, T. M., & Flamariquei, I. N. 1997: Hatching success and larval survival of the frogs *Hyla regilla* and *Rana aurora* under ambient and artificially enhanced conditions. Can. J. Zool. **75**, 1081—1088.

Peterson, J. A. & Blaustein, A. R. 1991: Unpalatability in anuran larvae as a defense against natural salamander predators. Ethol. Ecol. Evol. **3**, 63—72.

Tevini, M. (ed.) 1993: UV-B Radiation and Ozone Depletion. Lewis Publishers, Boca Raton, FL.
Walls, S. C., Blaustein, A. R. & Beatty, J. J. 1992: Amphibian biodiversity of the Pacific Northwest with special reference to old-growth stands. Northwest Environ. J. **8**, 53—69.
Worrest, R. C. & Kimeldorf, D. J. 1976: Distortions in amphibian development induced by ultraviolet-B enhancement (290—315nm) of a simulated solar spectrum. Photochem. Photobiol. **24**, 377—382.

Received: September 23, 1999

Initial acceptance: December 20, 1999

Final acceptance: April 18, 2000 (J.-G. Godin)