

Garter Snake Distributions in High-Elevation Aquatic Ecosystems: Is There a Link with Declining Amphibian Populations and Nonnative Trout Introductions?

KATHLEEN R. MATTHEWS,^{1,2} ROLAND A. KNAPP,³ AND KAREN L. POPE¹

¹USDA Forest Service, Pacific Southwest Research Station, Post Office Box 245, Berkeley, California 94701, USA

³Sierra Nevada Aquatic Research Laboratory, University of California, Star Route 1, Box 198, Mammoth Lakes, California 93546 USA

ABSTRACT.—The dramatic amphibian population declines reported worldwide likely have important effects on their predators. In the Sierra Nevada, where amphibian declines are well documented and some are closely tied to the introduction of nonnative trout, the mountain garter snake, *Thamnophis elegans elegans*, preys predominately on amphibians. We surveyed 2103 high-elevation lakes in the Sierra Nevada, quantified the distributional relationship between the mountain garter snake and anuran amphibians (*Pseudacris regilla*, *Rana muscosa*, and *Bufo* spp.) and used this information to evaluate the possibility that amphibian declines lead to declines of garter snakes. We observed a strong association between amphibian presence and garter snake presence. The probability of finding snakes in lakes with amphibians was 30 times greater than in lakes without amphibians. Lakes with snakes had higher numbers of amphibians within 1 km (mean = 4018.8) than did lakes without snakes (mean = 642.1). On a landscape scale, in Kings Canyon National Park (where 40% of larger lakes contain nonnative trout) amphibians were found in 52% of lakes, and 62 garter snakes were found in 33 of the 1059 lakes surveyed. In contrast, in the John Muir Wilderness (JMW; where 80% of larger lakes contain nonnative trout), amphibians were found in 19% of lakes, and no snakes were found in any of the 1044 lakes surveyed. Based on these data, we suggest that the introduction of nonnative trout has led not only to the decline of amphibians but also to the decline of garter snakes. This study supports the hypothesis that the presence of amphibians is a prerequisite for garter snake persistence in high-elevation portions of the Sierra Nevada and that the introduction of trout into an ecosystem can have serious effects, not just on their prey but also on other predators in the ecosystem.

Recent reports of amphibian declines throughout the world (Blaustein and Wake, 1990; Halliday, 1998; Houlihan et al., 2000) have resulted in many studies of potential causes of the declines (Blaustein et al., 1994; Berger et al., 1998; Marco et al., 1999; Knapp and Matthews 2000a). Despite the growing body of research, little is known regarding the impact of the declines on other species in the ecosystem. Theory predicts that species declines will likely have ramifications throughout the food web (MacArthur, 1955; De Angelis, 1975; Pimm, 1980). These effects may be particularly marked on the predators that rely on the species removed, especially when there is limited alternative prey available (Paine, 1966; Lynch, 1979; Pimm, 1980). Therefore, we anticipate that the dramatic declines of amphibian populations in some ecosystems have caused declines in predators that rely on amphibians as their primary prey.

In the Sierra Nevada of California, there is considerable evidence that several species of amphibians have declined or disappeared from some regions (Bradford, 1991; Drost and Fellers,

1996; Knapp and Matthews, 2000a). Amphibians were ubiquitous vertebrates within the historically fishless aquatic habitats of the high Sierra Nevada (e.g., Grinnell and Storer, 1924). However, within the past century, trout have been introduced to the majority of large water bodies of the high Sierra and are at least partially responsible for the dramatic declines in some amphibian populations (Knapp and Matthews, 2000b). For example, recent studies (Bradford, 1989; Bradford et al., 1993; Knapp and Matthews, 2000a) have documented that the once common mountain yellow-legged frog, *Rana muscosa*, has declined in the Sierra Nevada in large part because of the introduction of nonnative trout. On a landscape scale (surveys of > 1700 lakes over 100,000 ha), Knapp and Matthews (2000a) found *R. muscosa* were more abundant in Kings Canyon National Park (KCNP) where introduced fish are less common compared to the adjacent John Muir Wilderness (JMW) where introduced fish are abundant.

One common native predator of amphibians in the Sierra Nevada is the mountain garter snake, *Thamnophis elegans elegans* (Grinnell and Storer, 1924; Mullally and Cunningham, 1956; Jennings et al., 1992). California museum collec-

² Corresponding Author. E-mail: kmatthews@fs.fed.us

tions from the 1800s and early 1900s show that mountain garter snakes ranged throughout the Sierra Nevada in addition to high elevations of the San Bernardino Mountains (U.C. Berkeley Museum of Vertebrate Zoology records, California Academy of Sciences Herpetology Collection). In the high Sierra Nevada (> 2000 m), habitat of *T. e. elegans* is restricted and the snakes are primarily found in streams, lakes, and wet meadows where they feed predominately on amphibians (Grinnell and Storer, 1924). Indeed, researchers have speculated that the presence of amphibians might be prerequisite for *T. e. elegans* existence in the high Sierra (Jennings et al., 1992) where long winters and overall low temperatures preclude other snakes from occurring above about 2500 m (Basey, 1991). Moreover, Jennings et al. (1992) proposed that as local amphibian populations decline or become extinct, *T. e. elegans* might also disappear. If these hypotheses are correct, then garter snakes would more likely be found in areas with high numbers of amphibians and would also more likely be found in KCNP than in the JMW where amphibians have declined more dramatically (Knapp and Matthews 2000a).

We used analyses based on surveys of over 2000 water bodies in a 130,000 ha area of the JMW and the adjacent KCNP to describe the relationship between current garter snake distributions and amphibian distributions on a local and landscape scale. We first quantified the relationship between garter snake presence in lakes and amphibian presence and abundance and then used the current information on amphibian distributions in the JMW and KCNP to evaluate whether the large scale declines of amphibians described for JMW has led to fewer garter snakes, as predicted by Jennings et al. (1992).

MATERIALS AND METHODS

As part of a larger study to determine the effect of introduced trout on native biota (Matthews and Knapp, 1999; Knapp and Matthews, 2000a), we surveyed 2103 lakes and ponds (all will be referred to as lakes) in the JMW and KCNP (Fig. 1) between 1995 and 1997. Lakes were identified from U.S. Geological Survey (USGS) 1:24,000 topographic maps and included 1044 and 1059 lakes in the JMW and KCNP study areas, respectively. All lakes were visited and surveyed within the 130,000 ha study area. The JMW and KCNP study areas are adjacent protected areas which were historically fishless (Fig. 1; Knapp, 1996) and are generally similar in habitat except that there are more lakes with introduced trout in the JMW than in KCNP (Knapp and Matthews, 2000a). Aerial trout stocking continues in the JMW which is man-

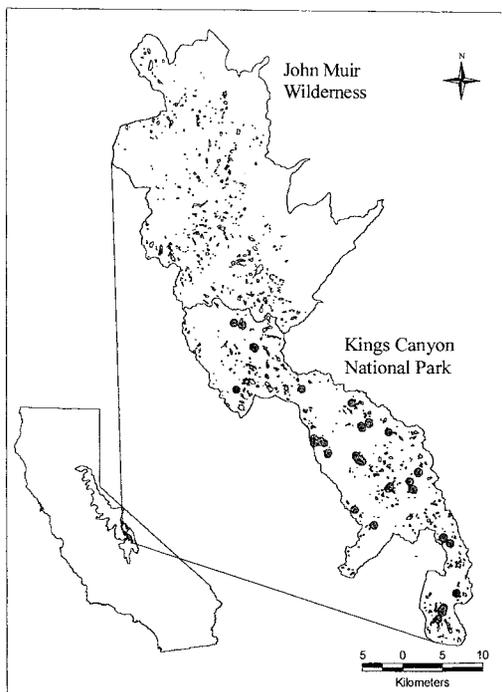


FIG. 1. Map of lakes surveyed within the John Muir Wilderness and Kings Canyon National Park study areas. The dark circles surround the lakes where garter snakes were found. The inset map shows the state of California, the historically fishless area of the Sierra Nevada, and the study areas in gray.

aged by the U.S. Forest Service but trout stocking was phased out in Kings Canyon National Park starting in the late 1970s. Lakes in the two alpine study areas both average 3400 m in elevation and have similar physical and chemical characteristics (Knapp and Matthews, 2000a) resulting from their common glacial origin and their location in watersheds dominated by intrusive igneous bedrock (California Division of Mines and Geology, 1958; Melack et al., 1985). With the exception of introduced fishes and low impact recreation, both areas are relatively undisturbed.

Surveys were conducted during the summer months when lakes were ice-free and amphibians, fish, and snakes were active. The species and number of amphibians and snakes at each lake was determined using visual encounter surveys (Crump and Scott, 1994). Each surveyor walked the shoreline of the entire lake or pond during daylight hours, noted the time, temperature, and species and number of snakes and amphibians. We counted the number of larval, subadult, and adult amphibians, and the presence and number of snakes. Some surveys were conducted during the early morning or evening

hours when chances of observing *T. e. elegans* and *R. muscosa* were lower (Gibson and Falls, 1979; Rossman et al., 1996; Pope, 1999); thus, we presumably underestimated their true numbers. To determine whether similar weather conditions (which may affect survey numbers of amphibians and reptiles) existed between the JMW and KCNP in the different years surveyed, we compared the air temperatures at the time of the surveys. Potential amphibians in the sampled lakes were *R. muscosa*, *Pseudacris regilla*, *Bufo canorus*, and *Bufo boreas*. Amphibians were identified to species except for *Bufo canorus* and *B. boreas*, which were combined into *Bufo* spp. caused by the difficulty of distinguishing the larval forms of the two species.

The presence or absence of trout (*Oncorhynchus mykiss* × *Oncorhynchus mykiss aguabonita* hybrids, *Salvelinus fontinalis*, and *Salmo trutta*) was determined at each lake using visual encounter surveys or gillnets. In shallow lakes (< 3 m deep) in which the entire bottom could be seen, trout presence or absence was determined using visual encounter surveys conducted while walking the entire shoreline and the first 100 m of each inlet and outlet stream. In deeper lakes, we determined fish presence or absence and species composition using a single monofilament gill net set for 8–12 h.

Analyses.—We conducted analyses at both the scale of individual lakes and at the landscape scale by comparing the JMW and KCNP study areas. To determine the general relationship between the presence/absence of snakes and amphibians at the lake scale, we used chi-square tests to determine whether the proportion of lakes containing amphibians differed between lakes where snakes were found and lakes where snakes were not found. Separate chi-square tests were also performed for lakes with specific amphibian species (*R. muscosa* only, *P. regilla* only, or both *R. muscosa* and *P. regilla*). We also tested whether the proportion of lakes containing trout differed between lakes with snakes and lakes without snakes.

Also at the lake scale, we used logistic regression (Cleveland and Devlin 1988; Hastie and Tibshirani, 1991) to determine the relationship between garter snake presence in lakes and amphibian presence while simultaneously accounting for the effects of potentially confounding variables (trout presence, elevation, lake area, and lake depth) that have been shown to be related to amphibian presence or absence (Pope, 1999; Knapp and Matthews, 2000a). Because no snakes were found in the JMW (see Results), we only used KCNP lakes for this analysis. We used the likelihood ratio statistic and Akaike information criteria (AIC; Linhart and Zucchini, 1986) to determine the significance

and relative importance of each covariate in the presence of all other covariates. After accounting for the effects of all observed significant habitat variables, we used the odds ratio (Hastie and Tibshirani, 1991) to determine the difference in the odds of finding *T. e. elegans* in the presence versus absence of amphibians. We also used the 1059 KCNP lakes to develop a generalized additive model (nonparametric linear regression) to quantify the relationship between the total number of snakes in a lake and the total number of amphibians while accounting for the effects of elevation, trout presence, and lake area using the equation

$$N_s \sim \text{trout presence/absence} + \text{lo}[\log(\text{amphibians} + 0.5)] + \text{lo}(\text{elevation}) + \text{lo}[\log(\text{lake area})]$$

where N_s = number of garter snakes found in a lake and $\text{lo}(\cdot)$ is the nonparametric loess smooth function. All regression-related calculations were made using S-Plus 2000 (MathSoft, Seattle, WA, 1999).

In addition to testing whether garter snake presence/absence in a lake is related to amphibian presence in the same lake, we also tested whether garter snakes were found in areas with higher numbers of amphibians (larvae, subadults, and adults). To test the prediction that garter snakes would be more likely to be found in areas with higher amphibian numbers, we compared the number of amphibians in a 1 km radius of the 33 lakes where garter snakes were found versus the number of amphibians found within 1 km of the 33 random lakes not inhabited with garter snakes. Using ArcView 3.1 (ESRI, Redlands, CA, 1996), we encircled areas surrounding each of the 33 garter snake lakes (1 km radius starting at the center of the garter snake containing lake), and 33 randomly chosen lakes lacking snakes in KCNP, and enumerated all amphibians found in the lakes within the circles. We then computed the total number of amphibians within all circles, and compared (*t*-test, $\alpha = 0.05$) the mean number of amphibians per zone around lakes with snakes to the mean number of amphibians in the randomly chosen lake zones. We chose the 1 km radius distance because, although little is known regarding *T. e. elegans* movement distances, studies of *R. muscosa* movement distances (Matthews and Pope, 1999; Pope, 1999) show that movement is typically less than 1 km and restricted within basins. Therefore, if garter snake distribution is related to amphibian distribution in the high Sierra, their movements may be similarly restricted.

At the landscape scale, we compared the number of snakes found in a region characterized by more severe amphibian declines (JMW) to a region with less severe amphibian declines

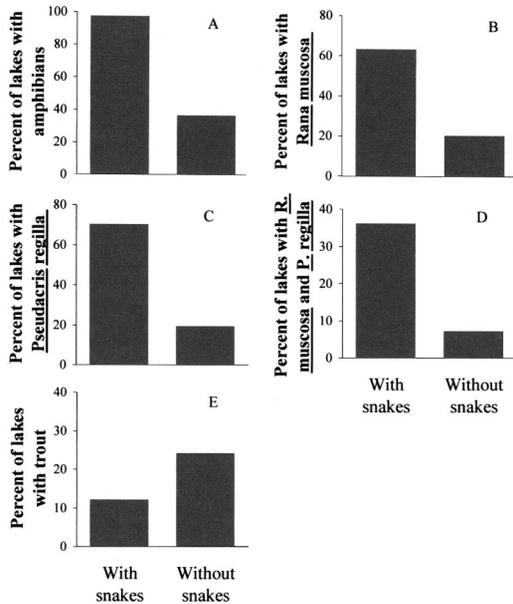


FIG. 2. Comparison of the percentage of surveyed lakes with amphibian species (A), *Rana muscosa* (B), *Pseudacris regilla* (C), *Rana muscosa* and *Pseudacris regilla* (D), and trout (E) in the 33 lakes where snakes were found and the 2070 lakes in the total study area (JMW and KCNP) where snakes were not found.

(KCNP). We first compared the proportion of lakes with amphibians in KCNP versus JMW (chi-square test) and then compared number of snakes found in the two regions.

RESULTS

A total of 62 garter snakes were found in 33 of the 1059 lakes surveyed in KCNP, and no snakes were found in the 1044 JMW lakes. The occurrence of garter snakes in a particular lake was closely linked to the presence of amphibians: of the 33 lakes with garter snakes, 97% also contained amphibians. In contrast, only 36% of lakes without garter snakes contained amphib-

ians (Fig. 2A; $\chi^2 = 80.8$, $P < 0.001$). An assessment of the association between snakes and specific amphibian species indicated that 64% of lakes with snakes also contained *R. muscosa* either alone or with other amphibians. In contrast, only 20% of lakes without snakes contained *R. muscosa* (Fig. 2B; $\chi^2 = 36.1$, $P < 0.001$). Moreover, 70% of lakes with snakes contained *P. regilla* either alone or with other amphibian species versus 19% of lakes without snakes (Fig. 2C; $\chi^2 = 50.6$, $P < 0.001$), and 36% of lakes with snakes contained both *R. muscosa* and *P. regilla* together versus 6% of lakes without snakes (Fig. 2D; $\chi^2 = 23.2$, $P < 0.001$). *Bufo* spp. were rare in the study areas (found in $< 0.4\%$ of all lakes surveyed) and were only seen in one KCNP lake with snakes (1300 tadpoles) and, therefore, were not included in the analyses. Finally, a negative association was found between snake presence and trout presence: 24% of trout-free lakes also contained snakes while only 12% of trout-containing lakes contained snakes (Fig. 2E; $\chi^2 = 4.1$, $P = 0.04$).

Garter snakes did not associate disproportionately with *R. muscosa* versus *P. regilla* ($\chi^2 = 0.6$, $P = 0.45$) but did disproportionately associate with *R. muscosa* and *P. regilla* together versus either species alone ($\chi^2 = 27.2$, $P < 0.001$).

The logistic regression analysis of the study lakes in KCNP ($N = 1059$) indicated that the probability of snake presence was positively associated with presence of amphibians ($P < 10^{-6}$), negatively associated with elevation ($P < 0.001$), and positively associated with lake area ($P = 0.004$; Table 1). No other significant relationships were observed when all other variables were included (Table 1). After controlling for elevation and lake area, the probability of finding *T. e. elegans* in lakes with amphibians was 30 times greater than in lakes without amphibians (approximate 95% confidence limits: 3.7–238.7). The high variability in the confidence limits is likely due to the overall low number of snakes observed. Total snake numbers in lakes

TABLE 1. Test statistic, statistical significance (P -value), AIC values and direction of effect of the variables in the logistic regression model assessing the probability of finding *Thamnophis elegans elegans* at a lake. Variables ordered by relative significance determined by AIC value.

Variable	Test statistic ^a	df	P -value	AIC ^b	Direction of effect
Amphibian presence/absence	24.2	0.8	5.7×10^{-7}	267.7	+
Elevation	18.9	4.1	8.9×10^{-4}	255.9	-
Lake area*	15.6	4.2	0.004	252.4	+
Maximum depth	7.5	3.5	0.08	245.8	-
Fish presence/absence	2.1	0.9	0.14	244.6	NA

^a Test statistic = log likelihood ratio statistic.

^b AIC = Akaike information criteria = -2 (max. log likelihood) + 2 (number of parameters).

* Log-transformed.

TABLE 2. Test statistic (F -value) and statistical significance (P value) of the variables in the linear regression model for total number of snakes in a lake in Kings Canyon National Park ($N = 1059$; $df_1 = 1055$ and $df_2 = 1$ for all variables).

Variable	F -value	P -value	Direction of effect
Total amphibians*	24.0	1.1×10^{-6}	+
Elevation	11.5	7.2×10^{-4}	-
Lake area*	6.4	0.01	+
Fish presence/absence	2.6	0.11	-

* Log-transformed.

in KCNP were also positively associated with total amphibian numbers (linear regression, $P < 10^{-5}$) after accounting for possible habitat and trout effects (Table 2).

An examination of the 1-km zones surrounding lakes with and without garter snakes in KCNP indicated that zones containing garter snakes ($N = 33$) had more amphibians than did randomly chosen zones ($N = 33$) without snakes (mean = 4018.8 versus 642.1, respectively, t -test; $P < 0.001$).

On a landscape scale, amphibians were found in a higher proportion of lakes in KCNP (52%) than in the JMW (19%; $\chi^2 = 249.2$, $P < 0.0001$). In support of the hypothesis that garter snake distribution will be affected by amphibian declines, we found 62 garter snakes in KCNP (3.1% of surveyed lakes), whereas no garter snakes were observed in the JMW. We found no difference in air temperatures (14°C median for both KCNP and the JMW: Mann-Whitney rank sum, $P = 0.463$) during surveys conducted in the different years.

DISCUSSION

Our results indicate a strong relationship between garter snakes and amphibians in the aquatic ecosystems of the high-elevation Sierra Nevada and lend support to the prediction of Jennings et al. (1992) that amphibian declines will lead to garter snake declines. At the local scale, we found that garter snake presence in lakes was positively associated with presence and numbers of amphibians. At the landscape scale, we did not find any snakes in the JMW where dramatic amphibian declines have been reported and are at least partially attributed to the high proportion of lakes containing nonnative trout (Knapp and Matthews, 2000a). In contrast, we found garter snakes in the immediately adjacent KCNP where amphibian declines are less severe and a smaller proportion of lakes contain introduced trout. Although 19% of JMW lakes do contain amphibians, this likely represents a dramatic decline from the historic dis-

tributions and the remaining populations may not be adequate to support snakes.

One explanation for the snake distributional patterns we observed is that nonnative trout may prey on snakes and could therefore contribute directly to their decline. Indeed, snakes were found less often in lakes containing trout, but this finding is confounded by the fact that trout-containing lakes were also significantly less likely to contain amphibians (Knapp and Matthews 2000a). We never observed any fish-snake interactions in our surveys of 2103 lakes, and in qualitative inspections of more than 1200 fish stomachs in our lake surveys (RK and KM, unpubl. data) we never found any snakes. Moreover, in contrast to the highly significant effect of amphibian presence on snake presence, the presence of trout was not a significant predictor of garter snake presence/absence in our regression analyses. Therefore, we suspect that the distribution of amphibian prey may be the primary factor determining snake distribution and abundance among lakes. However, we cannot exclude the possibility that trout occasionally prey directly on snakes.

Jennings et al. (1992) found garter snakes primarily associated with *P. regilla* and *Bufo* spp., and never with *R. muscosa*, possibly because of the relatively small number of water bodies sampled (115). Based on their data, they speculated that *T. e. elegans* would not be affected by *R. muscosa* population changes because they were never found together. In our study, garter snakes were commonly associated with *R. muscosa*, and we suggest that the dramatic *R. muscosa* declines in the JMW are at least partially responsible for the lack of garter snakes observed in the JMW. We suspect that both the larger *R. muscosa* and smaller *P. regilla* are important prey for *T. e. elegans* depending on the snake's life-history stage because prey size preference often increases with garter snake size (White and Kolb, 1974; Macias Garcia and Drummond, 1988; Arnold, 1993). It also seems likely that smaller snakes rely more on *P. regilla* and *R. muscosa* tadpoles, whereas larger adult snakes rely more on subadult and adult *R. muscosa*.

Although garter snakes are reportedly opportunistic feeders (Kephart, 1982; Kephart and Arnold, 1982), garter snakes in high mountain lakes of the Sierra Nevada appear unable to switch to alternative prey following amphibian disappearances. Perhaps because high-elevation ecosystems are relatively species poor (Schoenherr, 1992), there are no suitable consistent and abundant alternative prey to sustain the snakes in the harsh environmental conditions (e.g., long, cold winters and short summers). Other typical prey eaten by garter snakes include in-

vertebrates, fishes, and small mammals (Rossman et al., 1996). Although fish are reported as being part of the diet of *T. elegans* in other areas (White and Kolb, 1974; Arnold, 1977; Kephart and Arnold, 1982), we never saw any evidence of garter snakes foraging on trout and rarely saw *T. e. elegans* in the same water body as trout. Researchers have reported that *T. elegans* is inept at capturing fish unless they are stranded in shallow water (Kephart and Arnold, 1982). In over 100 h of garter snake observations in Kings Canyon National Park, we have only observed garter snakes feeding on amphibians (about 20 observations), and have never observed them feeding on invertebrates, fish, or small mammals (KP and KM, unpubl. data). Nevertheless, a quantitative assessment of garter snake prey is needed.

Although fish stocking has long been thought of as a beneficial activity with few environmental consequences, it should be expected that a such a major perturbation across a large landscape would have a profound influence on food webs (Zaret and Paine, 1973; Crowder et al., 1996), especially in less complex ecosystems (Pimm, 1984). There is now considerable evidence of important landscape-scale consequences of the widespread fish introductions of predatory fish to native prey species such as zooplankton (Stoddard, 1987; Bradford et al., 1998; Knapp et al., 2001), amphibians (Bradford, 1989; Fisher and Shaffer, 1996) and benthic invertebrates (Bradford et al., 1998; Carlisle and Hawkins, 1998; Knapp et al., 2001). This study points out that introduced trout can also have serious effects on other predators in the ecosystem with whom they compete for prey, and that these impacts extend beyond the limits of the lake shorelines and into terrestrial habitats. Thus, in addition to the direct predatory effect of fish introductions on aquatic invertebrate and amphibian populations, fish introductions are further disrupting the high-elevation ecosystems of the Sierra Nevada by also affecting amphibian predators. Although beyond the scope of this study, we would also expect that the reduction of garter snakes in the high Sierra likely has additional impacts on their predators and other species in the ecosystem.

Acknowledgments.—We thank 23 field assistants for their help with data collection, D. Court and S. Mazzone for GIS support, H. Preisler for statistical assistance, B. Jennings for helpful comments on an earlier version of the manuscript, and L. Decker who was instrumental in obtaining funding for this project from the U.S. Forest Service's Region 5 Ecosystem Conservation Group. The research was also supported by the USFS Pacific Southwest Research Station.

LITERATURE CITED

- ARNOLD, S. J. 1977. Polymorphism and geographic variation in the feeding behavior of the garter snake *Thamnophis elegans*. *Science* 197:676–678.
- . 1993. Foraging theory and prey-size-predator-size relations in snakes. In R. A. Seigel and J. T. Collins (eds.), *Snakes: Ecology and Behavior*, pp. 87–115. McGraw-Hill, New York.
- BASEY, H. E. 1991. *Discovering Sierra Reptiles and Amphibians*. Yosemite Assoc. and Sequoia Natural History Association, Yosemite National Park, CA.
- BERGER, L., R. SPEARE, P. DASZAK, D. E. GREEN, A. A. CUNNINGHAM, C. L. GOGGIN, R. SLOCOMBE, 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 rain forests of Australia and Central America. *Proceedings of the National Academy of Sciences* 91:9031–9036.
- BLAUSTEIN, A. R., AND D. B. WAKE. 1990. Declining amphibian populations: A global phenomenon. *Trends in Ecology and Evolution* 5:203–204.
- BLAUSTEIN, A. R., P. D. HOFFMAN, G. D. HOKIT, J. M. KIESECKER, S. C. WALLS, AND J. B. HAYS. 1994. UV repair and resistance to solar UV-B in amphibian eggs: a link to population declines? *Proceedings of the National Academy of Sciences* 91:1791–1795.
- BRADFORD, D. F. 1989. Allotopic distribution of native frogs and introduced fishes in high Sierra Nevada lakes of California: implication of the negative effect of fish introductions. *Copeia* 1989:775–778.
- . 1991. Mass mortality and extinction in a high-elevation population of *Rana muscosa*. *Journal of Herpetology* 25:174–177.
- BRADFORD, D. F., F. TABATABAI, AND D. M. GRABER. 1993. Isolation of remaining populations of the native frog, *Rana muscosa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. *Conservation Biology* 7:882–888.
- BRADFORD, D. F., S. D. COOPER, T. M. J. JENKINS, K. KRATZ, O. SARNELLE, AND A. D. BROWN. 1998. Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2478–2491.
- CALIFORNIA DIVISION OF MINES AND GEOLOGY. 1958. *Geologic atlas of California*. California Department of Conservation, Sacramento.
- CARLISLE, D. M., AND C. P. HAWKINS. 1998. Relationships between invertebrate assemblage structure, 2 trout species, and habitat structure in Utah mountain lakes. *Journal of the North American Benthological Society* 17:286–300.
- CLEVELAND, W. S., AND S. J. DEVLIN. 1988. Locally weighted regression: an approach to regression analysis by local fitting. *Journal of the American Statistical Association* 83:596–610.
- CROWDER, L. B., D. P. REAGAN, AND D. W. FRECKMAN. 1996. Food web dynamics and applied problems. In G. A. Polis and K. O. Winemiller (eds.), *Food Webs: Integration of Patterns and Dynamics*, pp. 327–336. Chapman and Hall, New York.
- CRUMP, M. L., AND N. J. SCOTT JR. 1994. Visual encounter surveys. In W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, and M. S. Foster

- (eds.), *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*, pp. 84–91. Smithsonian Institution Press, Washington DC.
- DE ANGELIS, D. L. 1975. Stability and connectance in food web models. *Ecology* 56:238–243.
- DROST, C. M., AND G. M. FELLERS. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada. *Conservation Biology* 10: 414–425.
- FISHER, R. N., AND H. B. SHAFFER. 1996. The decline of amphibians in California's Great Central Valley. *Conservation Biology* 10:1387–1397.
- GIBSON, A. R., AND J. B. FALLS. 1979. Thermal biology of the common garter snake *Thamnophis sirtalis* (L.). I. Temporal variations, environmental effects and sex differences. *Oecologia* 43:79–83.
- GRINNELL, J., AND T. I. STORER. 1924. *Animal Life in the Yosemite*. University of California Press, Berkeley.
- HALLIDAY, T. R. 1998. A declining amphibian conundrum. *Nature* 394:418–419.
- HASTIE, T., AND R. TIBSHIRANI. 1991. *Generalized Additive Models*. Chapman and Hall, London.
- HOULIHAN, J. E., C. S. FINDLAY, B. R. SCHMIDT, A. H. MEYERS, AND S. L. KUZMIN. 2000. Quantitative evidence for global amphibian declines. *Nature* 404: 752–755.
- JENNINGS, W. B., D. F. BRADFORD, AND D. F. JOHNSON. 1992. Dependence of the garter snake *Thamnophis elegans* on amphibians in the Sierra Nevada of California. *Journal of Herpetology* 26:505–508.
- KEPHART, D. G. 1982. Microgeographic variation in the diets of garter snakes. *Oecologia* 52:287–291.
- KEPHART, D. G., AND S. J. ARNOLD. 1982. Garter snake diets in a fluctuating environment: a seven year study. *Ecology* 63:1232–1236.
- KNAPP, R. A. 1996. Non-native trout in the natural lakes of the Sierra Nevada: an analysis of their distribution and impacts on native aquatic biota. In *Sierra Nevada Ecosystem Project, Final Report to Congress*. Vol. 3. Center for Water and Wildland Resources, pp. 363–390. University of California, Davis.
- KNAPP, R. A., AND K. R. MATTHEWS. 2000a. Non-native fish introductions and the decline of the mountain yellow-legged frog from within protected areas. *Conservation Biology* 14:428–438.
- . 2000b. Effects of nonnative fishes on wilderness lake ecosystems in the Sierra Nevada and recommendations for reducing impacts. *Proceedings: Wilderness Science in a Time of Change*. Proceedings RMRS-P-15 Vol. 5:312–317. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- KNAPP, R. A., K. R. MATTHEWS, AND O. SARNELLE. 2001. Resistance and resilience of alpine lake fauna to fish introductions. *Ecological Monographs* 71:401–421.
- LINHART, H., AND W. ZUCCHINI. 1986. *Model selection*. John Wiley and Sons, New York.
- LYNCH, M. 1979. Predation, competition and zooplankton community structure: an experimental study. *Limnology and Oceanography* 24:253–272.
- MACARTHUR, R. 1955. Fluctuations of animal populations, and a measure of community stability. *Ecology* 36:533–536.
- MACIAS GARCIA, C., AND H. DRUMMOND. 1988. Seasonal and ontogenetic variation in the diet of the Mexican garter snake, *Thamnophis eques*, in Lake Tecocomulco, Hidalgo. *Journal of Herpetology* 22: 129–134.
- MARCO, A., C. QUILCHANO, AND A. R. BLAUSTEIN. 1999. Sensitivity to nitrate and nitrite in pond-breeding amphibians from the Pacific Northwest, USA. *Environmental Toxicology and Chemistry* 18: 2836–2839.
- MATTHEWS, K. R., AND R. A. KNAPP. 1999. A study of high mountain lake fish stocking effects in the U.S. Sierra Nevada Wilderness. *International Journal of Wilderness* 5:24–26.
- MATTHEWS, K. R., AND K. L. POPE. 1999. A telemetric study of the movement patterns and habitat use of *Rana muscosa*, mountain yellow-legged frog, in a high-elevation basin in Kings Canyon National Park, California. *Journal of Herpetology* 33:615–623.
- MELACK, J. M., J. L. STODDARD, AND C. A. OCHS. 1985. Major ion chemistry and sensitivity to acid precipitation of Sierra Nevada lakes. *Water Resources Research* 21:27–32.
- MULLALLY, D. P., AND J. D. CUNNINGHAM. 1956. Ecological relations of *Rana muscosa* at high elevations in the Sierra Nevada. *Herpetologica* 12:189–198.
- PAINE, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- PIMM, S. L. 1980. Food web design and the effect of species deletion. *Oikos* 35:139–149.
- . 1984. The complexity and stability of ecosystems. *Nature* 307:321–326.
- POPE, K. L. 1999. *Mountain Yellow-Legged Frog Habitat Use and Movement Patterns in a High Elevation Basin in Kings Canyon National Park*. Unpubl. master's thesis, California Polytechnic State University, San Luis Obispo.
- ROSSMAN, D. A., N. B. FORD, AND R. A. SEIGEL. 1996. *The Garter Snakes: Evolution and Ecology*. University of Oklahoma Press, Norman.
- SCHOENHERR, A. A. 1992. *A Natural History of California*. University of California Press, Berkeley.
- STODDARD, J. L. 1987. Microcrustacean communities of high-elevation lakes in the Sierra Nevada, California. *Journal of Plankton Research* 9:631–650.
- WHITE, M., AND J. A. KOLB. 1974. A preliminary study of *Thamnophis* near Sagehen Creek, California. *Copeia* 1974:126–136.
- ZARET, T. M., AND R. T. PAINE. 1973. Species introduction in a tropical lake. *Science* 182:449–455.

Accepted: 11 April 2001.