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Effects of nonnative fish and habitat characteristics on lentic herpetofauna in Yosemite National Park, USA

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Abstract

Nonnative fishes have been introduced into naturally fishless mountain lakes worldwide, often with negative consequences for native fauna. In this study, I used data collected during a census of native herpetofauna, nonnative trout, and habitat characteristics at all lentic water bodies in Yosemite National Park ($n = 2655$) to quantify the effect of trout introductions and habitat on the distribution of four amphibian species and two reptile species. Impacts of trout on amphibians and reptiles were characterized using generalized additive models that included as predictor variables fish presence/absence, amphibian presence/absence (only in models for the two reptile species), elevation, water depth, littoral zone and shoreline substrate composition, relative survey date, and location. All species showed significant associations with habitat characteristics, and elevation and water depth appeared particularly important in influencing distributions. In addition, distributions of the mountain yellow-legged frog (*Rana muscosa*) and Pacific treefrog (*Hyla regilla*) were strongly negatively associated with the presence of nonnative trout while those of the Yosemite toad (*Bufo canorus*) and Sierra newt (*Taricha torosa sierrae*) were unrelated to trout presence. The distribution of the mountain garter snake (*Thamnophis elegans elegans*) was strongly negatively associated with the presence of nonnative trout and positively associated with the presence of native amphibians. Regression results for the Sierra garter snake (*Thamnophis couchi couchi*) were similar except that the direct effect of nonnative trout was considerably weaker. Together, these results indicate that trout introductions have resulted in considerable alteration of Yosemite's herpetofauna. Long-term studies will be necessary to determine whether removal of nonnative trout populations, where possible, would allow these impacts to be partially reversed.

Keywords: Herpetofauna; Fish; Introduced species; Mountain lakes; Sierra Nevada

1. Introduction

The introduction of nonnative fishes has dramatically transformed extensive once-fishless montane landscapes throughout the world. For example, in the western US more than 60% of all naturally fishless lakes, many located within national parks and wilderness areas, now contain nonnative trout (Bahls, 1992). Predation on native fauna by these introduced trout frequently triggers profound ecological changes, including elimination of amphibian and reptile populations (Tyler et al., 1998; Knapp and Matthews, 2000; Matthews et al., 2001; Pilliod and Peterson, 2001), changes in zooplankton and benthic macroinvertebrate species composition and size structure (Anderson, 1980; Stoddard, 1987; Bradford et al., 1998; Knapp et al., 2001) and alteration of ecosystem processes such as nutrient cycling (Leavitt et al., 1994; Schindler et al., 2001).

Although the current body of literature describing the impacts of nonnative trout on native fauna is relatively extensive, nearly all of these studies focused solely on high elevation alpine lakes, the simple habitat structure of which may exacerbate the effects of fish predation (Savino and Stein, 1982; Anderson, 1984; Diehl, 1992). In contrast, lower elevation lakes often have considerable structural complexity, including abundant down logs and aquatic vegetation. If this increased habitat complexity reduces the intensity of trout predation, the impacts of introduced trout in these lakes may be markedly different than is suggested by the available literature.

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The primary objective of this study was to describe the effects of nonnative trout on the probability of site occupancy by four native amphibians and two native reptiles in Yosemite National Park, CA, USA. Lakes in Yosemite National Park span a wide elevational gradient and include many water bodies in the lower elevation forested zone (1500–2500 m). I quantified the effects of nonnative trout using regression models based on faunal and habitat surveys conducted at all of Yosemite's 2655 lentic water bodies. A secondary objective of this study was to describe the general habitat associations of the study species, as this information is either currently unavailable or is available only for the high elevation portions of the species' ranges (e.g., Matthews et al., 2001, 2002; Knapp et al., 2003).

2. Natural history of the study species

The study species include four amphibians and two snakes, all native to Yosemite National Park. The Yosemite toad (*Bufo canorus*) is endemic to a small portion of the central Sierra Nevada of California, including Yosemite National Park. The Pacific treefrog (*Hyla regilla*) is widespread throughout the western US, Baja California (Mexico), and southern British Columbia (Canada). The mountain yellow-legged frog (*Rana muscosa*) is endemic to the Sierra Nevada of California and Nevada and to the Transverse Ranges of southern California. The Sierra newt (*Taricha torosa sierrae*) is endemic to the Sierra Nevada's western slope (Stebbins, 1985). All four species breed in late spring in lakes, ponds, marshes, and slow-moving streams. However, while adult *B. canorus*, *H. regilla*, and *T. t. sierrae* frequent terrestrial habitats outside of the breeding season (Stebbins, 1985), adult *R. muscosa* are highly aquatic, rarely being found more than a few meters from water throughout the summer active season, and overwinter underwater (Zweifel, 1955; Matthews and Pope, 1999). In addition, *R. muscosa* larvae require two or more summers to reach metamorphosis (Bradford, 1989), instead of the one summer required by larvae of the other amphibian species. The only other lentic-breeding amphibian encountered during the study was the bullfrog (*Rana catesbeiana*), a nonnative species found at only five sites in the Park. Because of its nonnative status, it was not included in subsequent analyses. The Sierra garter snake (*Thamnophis couchi couchi*) is found primarily from central California to southern Oregon, and the mountain garter snake (*Thamnophis elegans elegans*) is found in the Sierra Nevada of California and Nevada (Stebbins, 1985). Both species were included in the current study because they depend heavily on amphibian prey and their population status may therefore be closely associated with that of amphibians (Jennings et al., 1992; Matthews et al., 2002). The Valley garter snake (*Thamnophis sirtalis fitchi*) and the Western pond turtle (*Clemmys marmorata*) were each found at only three sites in the Park and were therefore not included in subsequent analyses.

B. canorus and *R. muscosa* have both experienced dramatic population declines during the past century (Kagarise Sherman and Morton, 1993; Bradford et al., 1994; Drost and Fellers, 1996; Jennings, 1996), and their listing as "endangered" under the US Endangered Species Act was recently found to be warranted (Federal Register, 2002, 2003). The negative effect of introduced trout on *R. muscosa* is well-documented (Bradford, 1989; Bradford et al., 1998; Knapp and Matthews, 2000), but their effect on *B. canorus* is unknown. *H. regilla* may also have undergone some population declines (Drost and Fellers, 1996), perhaps caused in part by trout introductions (Matthews et al., 2001). However, this species remains widespread. *T. t. sierrae* has apparently not experienced declines and still occurs throughout its native range (Jennings, 1996). The status of *T. c. couchi* and *T. e. elegans* is poorly known, but some evidence suggests that *T. e. elegans* is declining in concert with its amphibian prey (Jennings et al., 1992; Matthews et al., 2002).

3. Methods

3.1. Study area description

Yosemite National Park (Fig. 1) encompasses 3027 km^2 of the central Sierra Nevada of California, USA (37°30′–38°11′N, 119°12′–119°53′E). Most of the Park is forested, and forest types range from mixed conifer stands at the lowest elevations (<2000 m) to montane forests at mid-elevations (2000–3000 m) to subalpine forests and alpine fell fields at the highest elevations (>3000 m) (Franklin and Fites-Kaufmann, 1996). Precipitation in Yosemite falls mostly in the winter months and is primarily rain at the lowest elevations and snow at the higher elevations.

Yosemite National Park contains >2000 lakes, ponds, and marshes, all located in watersheds dominated by intrusive igneous bedrock (California Division of Mines and Geology, 1958). Water body elevations range from 1079 to 3615 m, with a median elevation of 2786 m. These lentic habitats are generally small (<10 ha) and range from relatively warm water bodies at lower elevations that are typically surrounded by forest and often contain abundant aquatic vegetation, to high elevation, cold, oligotrophic water bodies surrounded by alpine meadows and rock. All natural lentic habitats in Yosemite were historically fishless as a result of numerous natural barriers at low elevation. Between 1870 and 1960, the majority of fishless lakes and streams were stocked with one or more species of trout (primarily

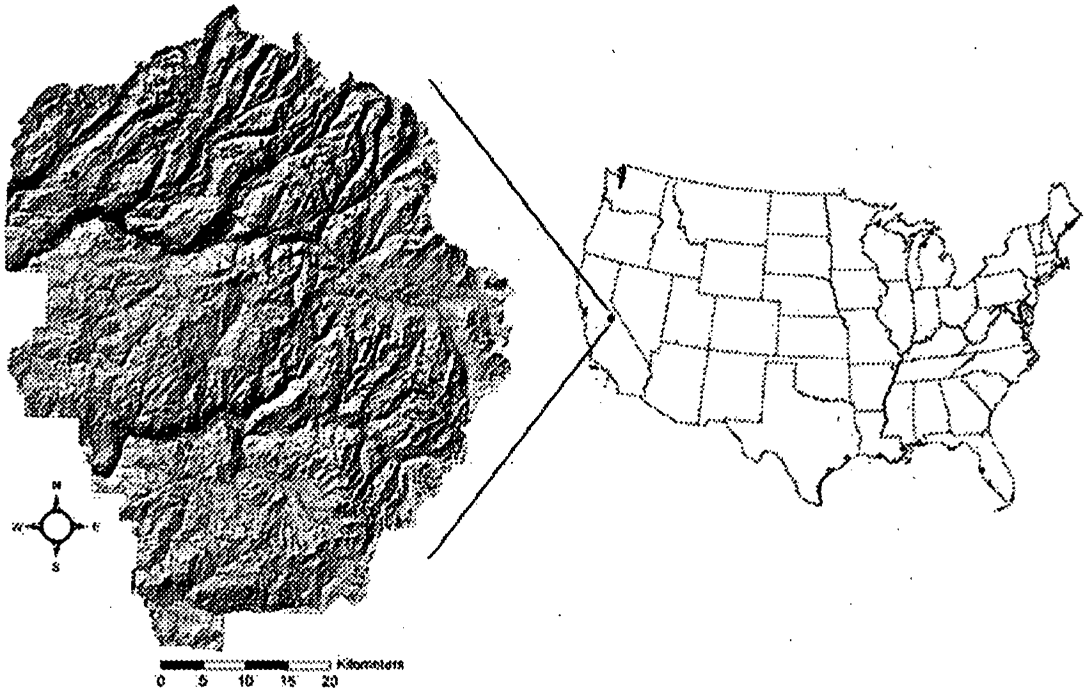

Fig. 1. Shaded relief map of the Yosemite National Park study area, the eastern border of which is the crest of the Sierra Nevada. Also shown is the location of study area within California, USA.

rainbow trout, *Oncorhynchus mykiss*, and brook trout, *Salvelinus fontinalis*) to create recreational fisheries. All fish stocking was halted in 1991 (Elliot and Loughlin, 1992), but trout have established reproducing populations in many previously stocked sites (Boiano, 1999) and remain widespread.

3.2. Amphibian, reptile, fish, and habitat surveys

All mapped lakes, ponds, and marshes in Yosemite National Park ($n = 2339$) were surveyed during single site visits made from 7 June to 30 September 2000, 9 June to 30 August 2001, or 4 June to 6 June 2002. Unmapped water bodies found while moving between mapped sites were also surveyed ($n = 316$). More than 99% of the sites were surveyed in 2000 and 2001, and during these years surveys were conducted by 2–3 crews per year, each made up of 2–3 people. In addition, all but one of the crew members in 2001 had also served as crew members in 2000. Crew members were trained on survey procedures and species identifications during a week-long period at the beginning of both field seasons. Precipitation during 2000, 2001, and 2002 was 103%, 75%, and 93% of the long-term average, respectively (California Department of Water Resources online report for Tuolumne Meadows, Yosemite National Park accessed on January 7, 2004; http://cdec.water.ca.gov/cgi-progs/snowQuery).

The presence/absence of each amphibian and reptile species at all water bodies was determined using visual encounter surveys (Crump and Scott, 1994) of the entire shoreline. Each species was determined to be present at a site if one or more egg masses, larvae, subadults (recently metamorphosed amphibians; snakes <20 cm in length), or adults were detected. *R. muscosa* is easy to detect using shoreline searches for two reasons. First, during the day adults spend the majority of their time on shore immediately adjacent to water and larvae are found primarily in near-shore shallows, making both life stages highly visible during shoreline surveys. Second, larvae are present throughout the summer (and during all other seasons) due to the unusual longevity of this life stage in *R. muscosa* (Bradford, 1989). As a result, single surveys at sites allow accurate assessment of *R. muscosa* presence/absence (Knapp and Matthews, 2000). Single surveys should also allow accurate assessment of presence/absence by *T. c. couchi* and *T. e. elegans* as individuals of these species are large (up to 100 cm), highly conspicuous, and are nearly always found on shore immediately adjacent to water. Single surveys are likely to be somewhat less accurate for *B. canorus*, *H. regilla*, and *T. t. sierrae*, however, due to the terrestrial habit of adults outside of the breeding season and their relatively short larval duration. However, because most surveys were conducted during the period when larvae and metamorphosing individuals of all three of these species are typically present, single site visits should still be reasonably effective at detecting them when they were present.

The presence/absence of trout was determined at each water body using visual encounter surveys or gill nets (Knapp and Matthews, 2000). In shallow water bodies (<3 m deep) in which the entire bottom could be seen, trout presence/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 water bodies, fish presence/absence was determined using both visual surveys and a single monofilament gill net set for 8–12 h (for gill netting details, see Knapp and Matthews, 1998).

I described the physical attributes of each water body using elevation, maximum water depth, and littoral zone (i.e., near-shore) and shoreline (i.e., terrestrial) substrate composition. Water body elevation (abbreviated as ELEV in Table 1) was obtained from USGS 1:24000 topographic maps. Maximum lake depth (DEPTH; Table 1) was determined by sounding with a weighted line. Littoral zone and shoreline substrate composition were characterized by visually estimating the dominant substrate along approximately 50 transects evenly spaced around the water body perimeter and placed perpendicular to the shoreline. Littoral zone substrates were characterized along transects extending from shore to 3 m into the water body, and substrates were categorized as silt (<0.5 mm), sand (0.5–2 mm), gravel (>2–75 mm), cobble (>75–300 mm), boulder (>300 mm), bedrock, or woody debris. Shoreline substrates were characterized along transects that extended from the water body edge to 1.5 m into the surrounding terrestrial zone. Shoreline substrates were categorized as silt/sand/gravel (0–75 mm), cobble (>75–300 mm), boulder/bedrock (>300 mm), grass/sedge/forb, or woody plants/debris. To reduce the dimensionality of the substrate data, I subjected the littoral zone and shoreline substrate data to separate principal components analyses. In both analyses, axis 1 explained a substantial amount of the total variation in substrate composition (littoral zone: 32%; shoreline: 33%), so was used as the independent variable representing littoral zone substrate composition (LPC1; Table 1) and shoreline substrate composition (SPC1; Table 1). Loadings of principal components axis 1 are shown in Table 2.

Table 2
Correlations of littoral zone and shoreline substrate categories with principal component axis 1

Substrate category	Axis 1
Littoral zone substrates	
Bedrock	−0.17
Boulder	−0.33
Cobble	−0.38
Gravel	−0.30
Sand	−0.30
Silt	0.57
Woody debris	0.01
Aquatic vegetation	0.46
Shoreline substrates	
Boulder/bedrock	−0.50
Cobble	−0.25
Silt/sand/gravel	−0.18
Woody plants/debris	−0.27
Grass/sedge/forb	0.76

All regression models also included a variable describing the relative survey date (number of days since January 1 – DAYS; Table 1) to account for the potentially confounding effect of species detectability changing over the summer. For example, a species might be easier to detect early in the summer (when adults are likely to be at breeding sites and larvae are present) than late in the summer (when many adults have moved into terrestrial habitats and larvae have metamorphosed).

3.3. Statistical analysis

Modeling efforts that make use of landscape-scale data are complicated by the fact that species distribution and associated habitat data are often spatially autocorrelated (Legendre, 1993), such that neighboring points are more similar than would be expected for randomly selected points. Spatially autocorrelated data cause problems for most statistical tests (e.g., generalized linear models) because these tests assume in-

Table 1
Description of predictor variables used in the generalized additive models

Variable name	Description
Fish presence/absence (FISH)	Presence/absence of nonnative trout as determined using visual and/or gill net surveys
Amphibian presence/absence (AMPHIB)	Presence/absence of native amphibians as determined using visual surveys
Water body elevation (m) (ELEV)	Elevation of water body as determined from USGS 1:24000 topographic maps
Water body depth (m) (DEPTH)	Maximum depth of water body as determined by sounding with a weighted line
Littoral zone substrate composition (LPC1)	First principal component for all littoral zone substrate types
Shoreline substrate composition (SPC1)	First principal component for all shoreline substrate types
Relative survey date (DAYS)	Date on which water body was surveyed, as the number of days since January 1
Water body location (LOCATION)	Smooth function of UTM easting and northing

Variable name abbreviations are given in parentheses.

dependence of error terms (Augustin et al., 1998). As a result, correct inference from spatially autocorrelated data is possible only by first extracting spatial dependencies or by explicitly modeling spatial autocorrelation (Legendre and Fortin, 1989). In this study, I used generalized additive models and extracted spatial dependencies by including a locational covariate (*X* and *Y* coordinates of each water body; LOCATION – Table 1) as a predictor variable (Hobert et al., 1997; Knapp et al., 2003). Generalized additive models (GAMs) are similar to generalized linear models, but relax the assumption that the relationships between the dependent variable (when transformed to a logit scale) and predictor variables are linear. Relaxation of this assumption is accomplished by estimating a nonparametric smooth function to describe the relationships between the dependent and predictor variables (Cleveland and Devlin, 1988; Hastie and Tibshirani, 1991).

The dependent variable in all regression models was the presence/absence of any life stage of the amphibian or reptile species of interest. I used presence/absence data instead of abundance data as the dependent variable because abundance data generally show much greater temporal fluctuations that do presence/absence data, and previous studies using similar data sets and statistical methods as those used in this paper have reported that models based on presence/absence data and abundance data produced very similar results (Knapp and Matthews, 2000; Matthews et al., 2001). In addition, I based the dependent variable on the presence of all life stages instead of only on those life stages that are indicative of breeding (egg masses, larvae, subadults) because preliminary analyses indicated that model results based on either dependent variable were virtually identical.

In multiple regression, multicollinearity between predictor variables may confound their independent effects. Therefore, prior to regression analysis I calculated Pearson correlation coefficients (*r*) for all pairwise combinations of predictor variables (Hair et al., 1998). Correlation coefficients ranged between −0.49 and 0.42 and were well below the suggested cutoff of $|r| \geqslant 0.85$ that would indicate collinearity for the sample size used in these analyses (Berry and Felman, 1985). Therefore, all predictor variables were included in the regression models.

In the regression models, p_i is the probability of finding the species at location *i*, and is defined as

$$p_i = \frac{e^{\theta_i}}{1 + e^{\theta_i}},$$

where the linear predictor (i.e., logit line) θ_i is a function of the independent variables. For all amphibian species, the specific relationship I used for θ_i was

$$\begin{aligned}\theta_i = {} & \mathrm{FISH} + g_1(\mathrm{DAYS}_i) + g_2(\mathrm{DEPTH}_i) \\ & + g_3(\mathrm{ELEV}_i) + g_4(\mathrm{LPC1}_i) + g_5(\mathrm{SPC1}_i) \\ & + g_6(\mathrm{LOCATION}). \qquad (1)\end{aligned}$$

Both garter snake species included in the current study are known to depend heavily on amphibian prey. Therefore, in the regression models for the two garter snakes I included the presence/absence of amphibians as an additional predictor variable (AMPHIB; Table 1). For the two reptile species, the specific relationship I used for θ_i was

$$\begin{aligned}\theta_i = {} & \mathrm{FISH} + \mathrm{AMPHIB} + g_1(\mathrm{DAYS}_i) \\ & + g_2(\mathrm{DEPTH}_i) + g_3(\mathrm{ELEV}_i) + g_4(\mathrm{LPC1}_i) \\ & + g_5(\mathrm{SPC1}_i) + g_6(\mathrm{LOCATION}). \qquad (2)\end{aligned}$$

In Eq. (1) and (2), $g(\cdot)$ represents a nonparametric smooth function that characterizes the effect of each continuous independent variable on the probability of response. The locational covariate (*g*(LOCATION)) was a smooth surface of UTM easting and northing (Table 1).

Regression methods were identical to those described in Knapp et al. (2003). Briefly, the nonparametric functions within each generalized additive model were estimated simultaneously using a loess smoother (Cleveland and Devlin, 1988). The best combination of independent variables was determined by evaluating the change in deviance resulting from dropping each variable from the model in the presence of all other variables. Analysis of deviance and likelihood ratio tests (based on the binomial distribution) were used to test the significance of the effect of each predictor variable on the probability of occurrence by each amphibian or reptile species (McCullagh and Nelder, 1989). Because the large sample sizes used in the regression models could result in predictor variables being statistically significant despite very weak associations with species presence/absence, predictor variables were considered to have significant effects only when $P \leqslant 0.01$. For all regression models, the relationship between the significant predictor variables and the probability of species occurrence is shown graphically in separate plots. Each plot depicts a response curve that describes the contribution of the predictor variable to the logit line. More generally, the response curve shows the relative influence of the predictor variable on the probability of species occurrence. This response curve is based on partial residuals, is plotted on a log-scale, and is standardized to have an average value of 0. For example, a hump-shaped response curve for the predictor variable, elevation, indicates that the amphibian or reptile species was, in a relative sense, most likely to be detected at sites at intermediate elevations and less likely to be detected at sites at both low and high elevations. All regression-related calculations were conducted using S-Plus (S-Plus, 2001).

4. Results

4.1. Nonnative fish

Introduced trout were observed in 245 of the 2655 surveyed water bodies (9%), and were found most commonly in water bodies deeper than 4 m (Fig. 2). Nonnative trout occupied 56% of these deeper habitats.

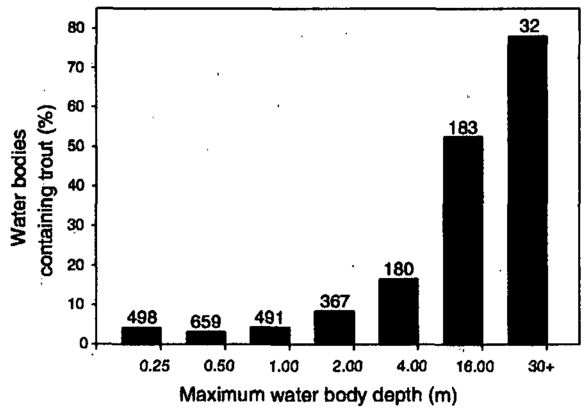

Fig. 2. Relationship between the percentage of water bodies containing nonnative trout and maximum water body depth. The number of water bodies in each depth category is given above the corresponding bar.

Gill net surveys indicated that brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*) were by far the most common fish species, with brown trout (*Salmo trutta*), golden trout (*O. mykiss aguabonita*), rainbow trout x golden trout hybrids, and Lahontan cutthroat trout (*O. clarki henshawi*) found only rarely ($\leqslant 3$ lakes each). The only other fish species encountered during the survey was an introduced population of Sacramento sucker (*Catostomus occidentalis*) detected at a single site.

4.2. Yosemite toad (*B. canorus*)

B. canorus was detected at 74 of the 2655 surveyed water bodies (3%). Univariate analysis indicated no significant difference in the probability of occurrence for *B. canorus* between sites at which nonnative trout were present versus absent (0.03 versus 0.02, respectively; χ^2 test: $\chi^2 = 0.62$, df = 1, $P = 0.43$). The generalized additive model also suggested that nonnative trout presence/absence was not associated with the probability of occurrence for *B. canorus* after accounting for the influence of other predictor variables (Table 3). Four of the six additional predictor variables (elevation, shoreline substrate composition, relative survey date, location) were significantly correlated with *B. canorus* occurrence (Table 3). The relationships between the probability of toad occurrence (on a logit scale) and the important continuously distributed predictor variables were all significantly nonlinear ($P < 0.03$; Fig. 3). The response curve describing the estimated effect of shoreline substrate composition on the probability of toad occurrence

Table 3
Results of generalized additive models developed for each amphibian and reptile species

Parameter	Amphibians				Reptiles	
	B. canorus	*H. regilla*	*R. muscosa*	*T. t. sierrae*	*T. c. couchi*	*T. e. elegans*
Null deviance	588	3651	1754	381	676	2104
Degrees of freedom (null model)	2654	2654	2654	2654	2654	2654
Model deviance[a]	380	2897	1294	147	310	1526
Degrees of freedom (full model)	2627	2627	2627	2627	2626	2626
Deviance increase[b]						
FISH	0.1 (0.05)$^{\mathrm{NS}}$	65 (8.6)***	64 (13.9)***	0.4 (0.2)$^{\mathrm{NS}}$	5 (1.2)$^{\mathrm{NS}}$	14 (2.4)*
AMPHIB	–	–	–	–	14 (3.8)*	88 (15.2)***
ELEV	22 (10.6)**	101 (13.4)***	46 (10.0)***	4 (1.7)$^{\mathrm{NS}}$	79 (21.6)***	47 (8.1)***
DEPTH	8 (3.8)$^{\mathrm{NS}}$	17 (2.2)*	120 (26.1)***	22 (9.4)*	9 (2.3)$^{\mathrm{NS}}$	55 (9.5)***
LPC1	3 (0.02)$^{\mathrm{NS}}$	61 (8.1)***	5 (0.01)$^{\mathrm{NS}}$	14 (6.0)*	5 (1.3)$^{\mathrm{NS}}$	9 (1.5)$^{\mathrm{NS}}$
SPC1	46 (22.1)***	36 (4.8)***	49 (10.6)***	6 (2.5)$^{\mathrm{NS}}$	6 (1.7)$^{\mathrm{NS}}$	3 (0.4)$^{\mathrm{NS}}$
DAYS	13 (6.2)*	48 (6.4)***	25 (5.4)**	12 (5.1)*	4 (1.2)$^{\mathrm{NS}}$	30 (5.2)**
LOCATION	34 (16.3)**	55 (7.3)***	145 (31.5)***	22 (9.4)*	23 (6.3)*	25 (4.3)*

[a] Sometimes referred to as "residual" deviance.

[b] Deviance increase: increase in deviance resulting from dropping the selected variable from the model. The percentage increase is given in parentheses, and was calculated as (deviance increase/(null deviance − model deviance)) × 100. Asterisks indicate the level of statistical significance associated with each variable.

$^{*}P \leqslant 0.01$.

$^{**}P \leqslant 10^{-4}$.

$^{***}P \leqslant 10^{-6}$.

NS, not significant ($P > 0.01$).

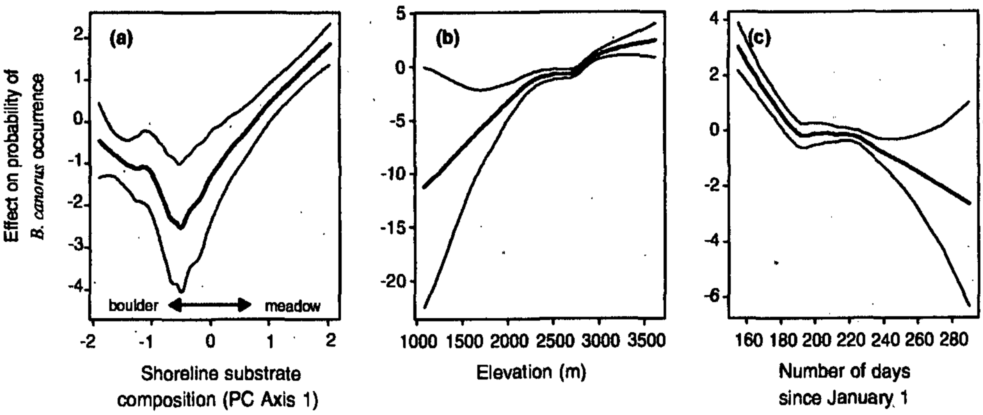

Fig. 3. Estimated effect of each of the highly significant ($P \leqslant 0.01$) predictor variables (including approximate 95% confidence intervals) on the probability of occurrence by *Bufo canorus*, as determined from the generalized additive model (span = 0.5). Variables are (a) shoreline substrate composition, (b) elevation, and (c) the number of days since January 1. Variables are displayed in order of decreasing importance.

(p_i) indicated that p_i was relatively constant and low at boulder-dominated sites (Table 2), but above a principal component axis 1 score of $-0.5 p_i$ increased steeply with increasing amounts of meadow vegetation on the water body shoreline (Fig. 3(a)). Toad occurrence was an increasing function of elevation (Fig. 3(b)). The response curve for relative survey date indicated that p_i decreased between early June and early July (number of days since January 1 = 155–190), and remained relatively low through early October (number of days since January 1 = 280; Fig. 3(c)). The response surface for water body location is not provided in this or subsequent figures as it was often complex and provided no additional insights into the effects of trout presence/absence or habitat effects on species occurrence.

4.3. Pacific treefrog (H. regilla)

H. regilla was detected at 1508 of the 2655 surveyed water bodies (57%). Univariate analysis indicated that *H. regilla* was detected much more often in water bodies lacking nonnative trout than in water bodies containing nonnative trout (0.58 versus 0.27, respectively; χ^2 test: $\chi^2 = 86.5$, df = 1, $P < 0.0001$). The generalized additive model also suggested that the probability of occurrence for *H. regilla* was strongly negatively associated with the presence/absence of nonnative trout after accounting for the influence of other predictor variables (Table 3; Fig. 4(b)). All six additional predictor variables (elevation, maximum water depth, littoral and shoreline zone substrate composition, relative survey date, location) also were significantly correlated with *H. regilla* occurrence (Table 3). The relationships between the probability of frog occurrence (on a logit scale) and the important continuously distributed predictor variables were all significantly nonlinear ($P < 0.002$) except that for littoral zone substrate composition ($P = 0.16$; Fig. 4). The response curve for elevation indicated that p_i was high and relatively constant from 1000 to 2800 m, but decreased sharply above 2800 m (Fig. 4(a)). For littoral zone substrate composition, the probability of *H. regilla* occurrence increased linearly with increasing principal component axis 1 score, indicating that p_i increased with increasing amounts of littoral zone silt and aquatic vegetation and decreased with increasing amounts of boulder, cobble, gravel, and sand (Fig. 4(c); Table 2). The response curve for relative survey date indicated that p_i was high and relatively constant from early June to early August (number of days since January 1 = 160–220) but decreased after early August (number of days since January 1 > 220; Fig. 4(d)). The response curve for shoreline substrate composition indicated that p_i was highest at intermediate principal component axis scores (Fig. 4(e)). The response curve for maximum water depth indicated that p_i increased sharply between water depths of 0 and 2 m and then remained relatively constant (Fig. 4(f)).

4.4. Mountain yellow-legged frog (R. muscosa)

R. muscosa was detected at 282 of the 2655 surveyed water bodies (11%). Univariate analysis indicated that *R. muscosa* was detected much more often at water bodies lacking nonnative trout than at water bodies containing nonnative trout (0.11 versus 0.02, respectively; χ^2 test: $\chi^2 = 18.78$, df = 1, $P < 0.0001$). The generalized additive model also suggested that the probability of occurrence for *R. muscosa* was strongly negatively associated with the presence/absence of nonnative trout after accounting for the influence of other predictor variables (Table 3; Fig. 5(b)). Five of the six additional predictor variables (elevation, maximum water depth, shoreline substrate composition, relative survey date, location) also were significantly correlated

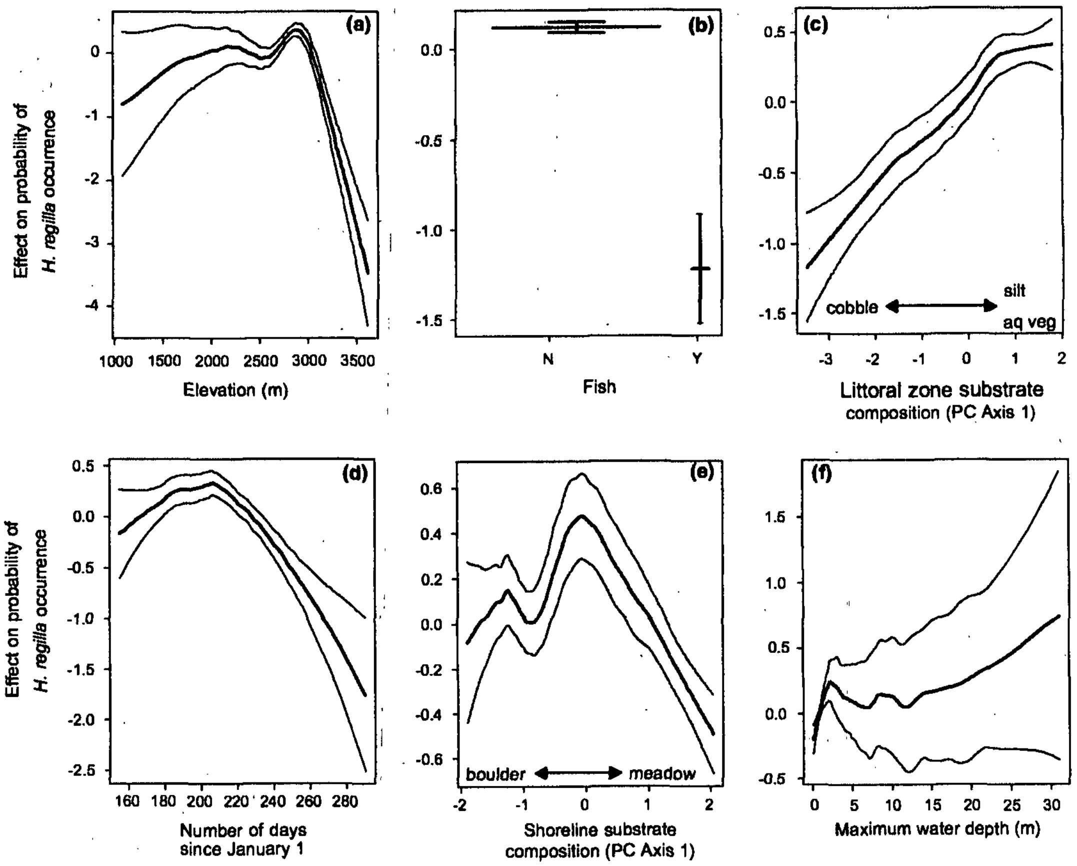

Fig. 4. Estimated effect of each of the highly significant ($P \leq 0.01$) predictor variables (including approximate 95% confidence intervals) on the probability of occurrence by *Hyla regilla*, as determined from the generalized additive model (span = 0.5). Variables are (a) elevation, (b) presence/absence of nonnative trout, (c) littoral zone substrate composition, (d) the number of days since January 1, (e) shoreline substrate composition, and (f) maximum water depth. Variables are displayed in order of decreasing importance.

with *R. muscosa* occurrence (Table 3). The relationships between the probability of frog occurrence (on a logit scale) and the important continuously distributed predictor variables were all significantly nonlinear ($P < 0.0001$) except that for shoreline substrate composition ($P = 0.82$; Fig. 5). The response curve for maximum water depth indicated that p_i increased sharply between 0 and 5 m and then remained high and relatively constant above 5 m (Fig. 5(a)). For shoreline substrate composition, the probability of frog occurrence increased linearly with increasing amounts of meadow vegetation on the water body shoreline (Fig. 5(c)). The response curve for elevation indicated that p_i increased steeply with increasing elevation up to approximately 2900 m, after which p_i remained high and relatively constant (Fig. 5(d)). The relationship between p_i and relative survey date was complex (Fig. 5(e)), and indicated that the probability of frog occurrence was high in early June (number of days since January 1 = 160), declined between early June and early July (160–185 days), increased between early July and early August (185–220 days), and then declined slightly after early August (>220 days).

4.5. Sierra newt (*T. t. sierrae*)

T. t. sierrae was detected at 37 of the 2655 surveyed water bodies (1%). Univariate analysis indicated no significant difference in the probability of occurrence for *T. t. sierrae* between sites at which nonnative trout were present versus absent (0.01 versus 0.02, respectively; χ^2 test: $\chi^2 = 0.47$, df = 1, $P = 0.49$). The generalized additive model also suggested that nonnative trout presence/absence was not associated with the probability of occurrence for *T. t. sierrae* after accounting for the influence of other predictor variables (Table 3). Four of the six additional predictor variables (maximum water depth, littoral zone substrate composition, relative survey date, location) were also significantly associated with *T. t. sierrae* occurrence (Table 3). The relationships between the probability of newt occurrence (on a logit scale) and the important

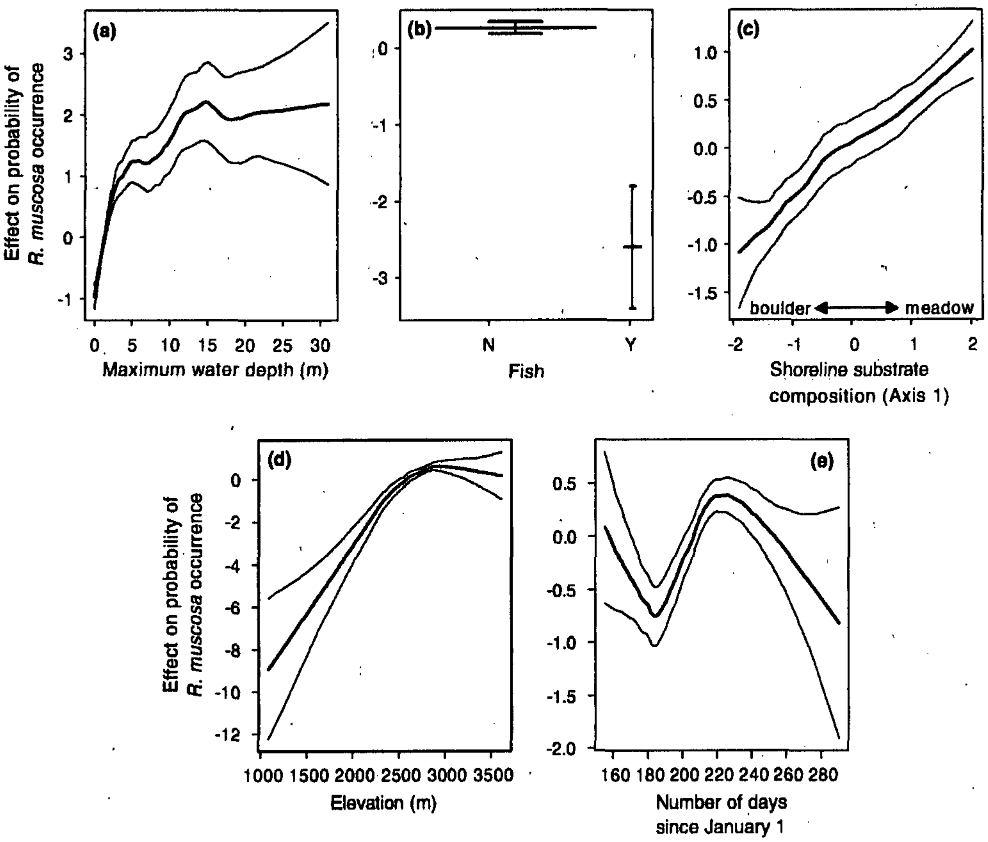

Fig. 5. Estimated effect of each of the highly significant ($P \leqslant 0.01$) predictor variables (including approximate 95% confidence intervals) on the probability of occurrence by *Rana muscosa*, as determined from the generalized additive model (span = 0.5). Variables are (a) maximum water depth, (b) presence/absence of nonnative trout, (c) shoreline substrate composition, (d) elevation, and (e) number of days since January 1. Variables are displayed in order of decreasing importance.

continuously distributed predictor variables were significantly nonlinear for maximum water depth and relative survey date ($P < 0.008$) and linear for littoral zone substrate composition ($P > 0.07$; Fig. 6). The response curve for maximum water depth indicated that p_i increased sharply between 0 and 3 m and then remained high and relatively constant for water bodies deeper than 3 m (Fig. 6(a)). For littoral zone substrate composition, the probability of newt occurrence decreased with increasing amounts of silt and aquatic vegetation (Fig. 6(b)). The response curve for relative survey date indicated that p_i was highest in early July (number of days since January 1 = 190) and lowest in early and late summer (Fig. 6(c)).

4.6. Sierra garter snake (*T. c. couchi*)

T. c. couchi was detected at 76 of the 2655 surveyed water bodies (3%). Univariate analysis indicated no significant difference in the probability of occurrence for *T. c. couchi* between sites at which nonnative trout were present versus absent (0.02 versus 0.03, respectively; χ^2 test: $\chi^2 = 0.90$, df = 1, $P = 0.34$). However, *T. c. couchi* was more likely to be found at water bodies containing amphibians than at water bodies lacking amphibians (0.04 versus 0.01, respectively; χ^2 test: $\chi^2 = 27.4$, df = 1, $P < 0.0001$). Similarly, the generalized additive model suggested that nonnative trout presence/absence had a marginally nonsignificant association ($P = 0.03$) and amphibian presence/absence had a highly significant association with the probability of occurrence for *T. c. couchi*, after accounting for the influence of the other predictor variables (Table 3; Fig. 7(b)). Two of the six additional predictor variables (elevation, location) were also significantly associated with *T. c. couchi* occurrence (Table 3). The relationship between the probability of snake occurrence (on a logit scale) and elevation was significantly nonlinear ($P < 0.02$), and indicated that p_i decreased sharply with increasing elevation (Fig. 7(a)). Because of the relatively small number of sites at which *T. c. couchi* was found during the survey, I was unable to analyze the separate effects of each amphibian species on the probability of snake occurrence.

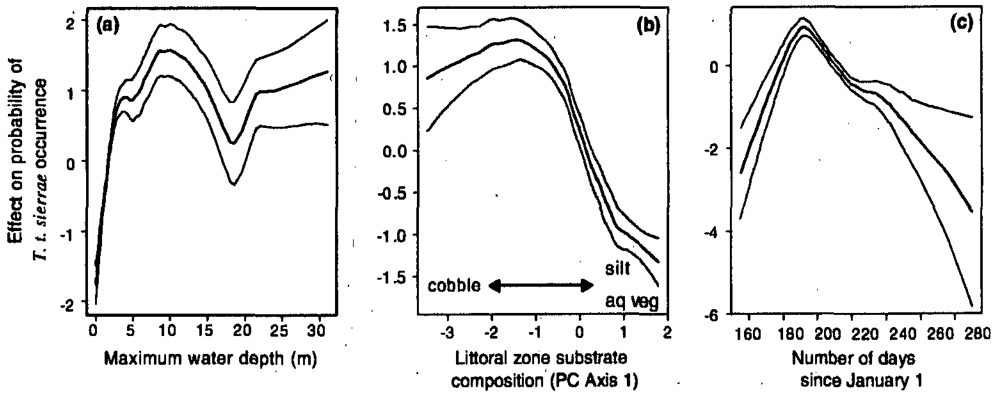

Fig. 6. Estimated effect of each of the highly significant ($P \leq 0.01$) predictor variables (including approximate 95% confidence intervals) on the probability of occurrence by *Taricha torosa sierrae*, as determined from the generalized additive model (span = 0.5). Variables are (a) maximum water depth, (b) littoral zone substrate composition, and (c) number of days since January 1. Variables are displayed in order of decreasing importance.

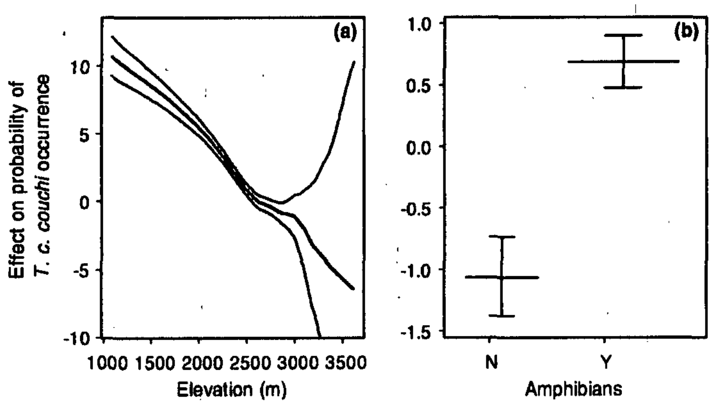

Fig. 7. Estimated effect of each of the highly significant ($P \leq 0.01$) predictor variables (including approximate 95% confidence intervals) on the probability of occurrence by *Thamnophis couchi couchi*, as determined from the generalized additive model (span = 0.5). Variables are (a) elevation, and (b) presence/absence of native amphibians. Variables are displayed in order of decreasing importance.

4.7. Mountain garter snake (*T. e. elegans*)

T. e. elegans was detected at 376 of the 2655 surveyed water bodies (14%). Univariate analysis indicated that *T. e. elegans* was much more likely to be found at water bodies lacking nonnative trout than at water bodies containing nonnative trout (0.14 versus 0.05, respectively; χ^2 test: $\chi^2 = 16.4$, df = 1, $P = 0.0001$). In addition, *T. e. elegans* was much more likely to be found at water bodies containing amphibians than at water bodies lacking amphibians (0.21 versus 0.02, respectively; χ^2 test: $\chi^2 = 188.0$, df = 1, $P < 0.0001$). The generalized additive model also suggested that the probability of occurrence for *T. e. elegans* was negatively associated with the presence/absence of nonnative trout (Table 3; Fig. 8(e)) and strongly positively associated with the presence/absence of amphibians (Table 3; Fig. 8(a)), after accounting for the influence of the other predictor variables. Four of the six additional predictor variables (elevation, maximum water depth, relative survey date, location) were also significantly associated with *T. e. elegans* occurrence (Table 3). The relationship between the probability of snake occurrence (on a logit scale) and the important predictor variables was significantly nonlinear for all important continuously distributed predictor variables ($P < 0.0004$; Fig. 8). The response curve for maximum water depth indicated that p_i increased sharply between depths of 0 and 5 m, and remained high and relatively constant for depths of 5–30 m (Fig. 8(b)). The response curve for elevation indicated that p_i was high and relatively constant at elevations of 1000–2600 m, but decreased sharply above 2600 m (Fig. 8(c)). The response curve for relative survey date indicated that p_i was highest in mid-August (number of days since January 1 = 230), and was lower earlier and later in the summer (Fig. 8(d)). Given that the presence of amphibians was strongly positively associated with *T. e. elegans* occurrence (Fig. 8(a)), I developed an

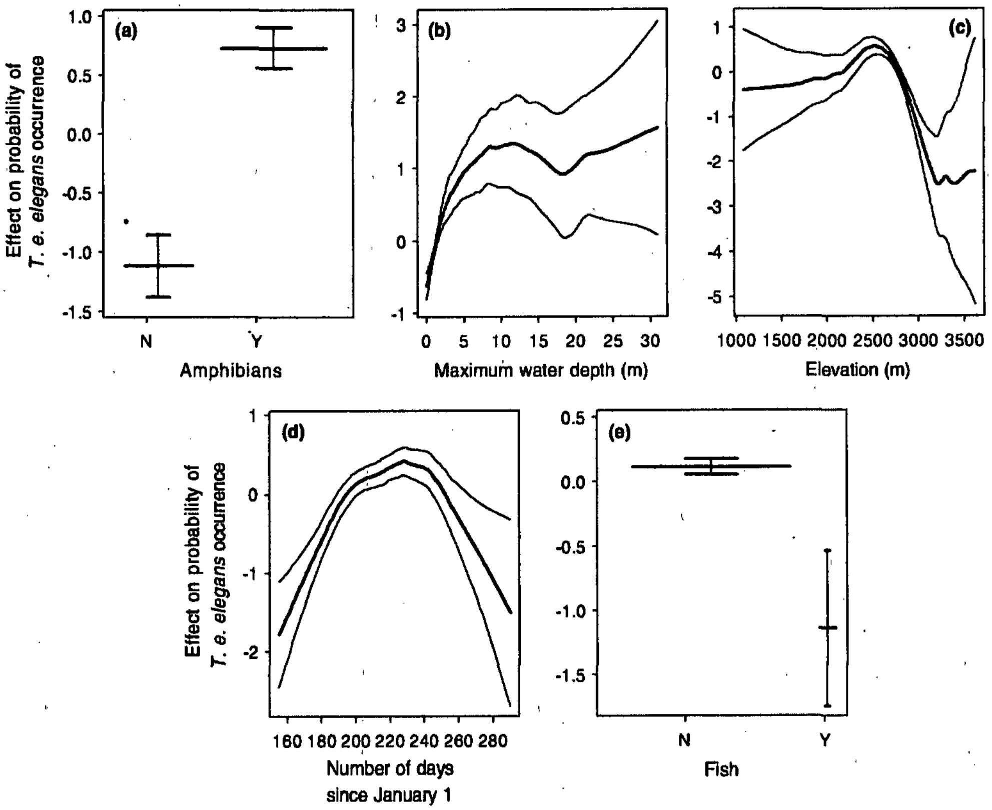

Fig. 8. Estimated effect of each of the highly significant ($P \leqslant 0.01$) predictor variables (including approximate 95% confidence intervals) on the probability of occurrence by *Thamnophis elegans elegans*, as determined from the generalized additive model (span = 0.5). Variables are (a) amphibian presence/absence, (b) maximum water depth, (c) elevation, (d) number of days since January 1, and (e) presence/absence of nonnative trout. Variables are displayed in order of decreasing importance.

additional regression analysis to evaluate the importance of particular amphibian species on the probability of occurrence by *T. e. elegans*. In this model, I substituted variables representing the presence/absence of *B. canorus*, *H. regilla*, *R. muscosa*, and *T. t. sierrae* for the AMPHIB variable. This analysis indicated that the importance of relative survey date, fish, and habitat variables remained unchanged, and that the presence/absence of *H. regilla* or *R. muscosa* both had highly significant effects on p_i ($P < 4.6 \times 10^{-7}$). In contrast, the presence/absence of *B. canorus* or *T. t. sierrae* did not have significant effects on p_i ($P > 0.2$).

5. Discussion

The introduction of fish into naturally fishless ecosystems is often suggested as a factor contributing to the worldwide decline of amphibian and reptile populations (Bradford, 1989; Jennings et al., 1992; Brönmark and Edenhamn, 1994; Braña et al., 1996; Gamradt and Kats, 1996; Fisher and Shaffer, 1996; Tyler et al., 1998; Pilliod and Peterson, 2001; Hamer et al., 2002; Matthews et al., 2002). The results of the current study provide strong evidence that in Yosemite National Park, introduced trout have profoundly altered the distribution of two of the four native aquatic-breeding amphibians and both of the widely distributed garter snake species.

5.1. Amphibians

Univariate and multivariate analyses indicated that the probability of occurrence for *H. regilla* and *R. muscosa* were both negatively associated with the presence of nonnative trout. These findings indicate that the strong negative association between trout and these two species that has been documented in the structurally simple lentic habitats of the high elevation southern Sierra Nevada (Bradford, 1989; Bradford et al., 1998; Knapp and Matthews, 2000; Knapp et al., 2001; Matthews et al., 2001; Knapp et al., 2003) also hold true in the structurally more complex lentic habitats characteristic of Yosemite National Park.

In contrast, univariate and multivariate analyses indicated that the probability of occurrence for *B. canorus* and *T. t. sierrae* was unrelated to the presence of nonnative trout. One possible reason for the lack of a negative association could be that the distributions of these two amphibians may not overlap with those of trout (e.g., amphibians in shallow ponds, trout in deep lakes; Drost and Fellers, 1996). This explanation appears unlikely to apply to either of these amphibian species, however. *B. canorus* occurred across nearly the entire range of water body depths available (0.1–14.5 m) and 11% of *B. canorus* populations occurred in water bodies $\geqslant$ 4 m deep. *T. t. sierrae* actually occurred disproportionately in deeper water bodies, with 38% of populations occurring in water bodies $\geqslant$ 4 m deep. Given that introduced trout in Yosemite are typically found in water bodies deeper than 4 m, *B. canorus* and *T. t. sierrae* may overlap with introduced trout more often than is commonly believed (e.g., Drost and Fellers, 1996). A more likely reason that the distributions of *B. canorus* and *T. t. sierrae* were unrelated to the presence/absence of nonnative trout is that toads and newts are generally distasteful or toxic (Brodie, 1968; Peterson and Blaustein, 1991; Crossland and Alford, 1998). The potential role for distastefulness in protecting *B. canorus* from trout predation is suggested by observations made during the field surveys in which *B. canorus* larvae were seen swimming in the pelagic zone of fish-containing lakes and in plain view of numerous brook trout (*Salvelinus fontinalis*) that made no attempt to prey on the larvae (Knapp and Moore, personal observations).

While the regression results suggest that trout have no effect on the distribution of *B. canorus* and *T. t. sierrae*, other more subtle impacts of trout are possible and should be explored further before a negative effect of trout on these species is totally discounted. First, it is possible that trout do prey on some life stages of these two species at a high enough level to influence population densities but not presence/absence. For example, trout readily prey on subadults of the closely related California toad (*Bufo boreas halophilus*) in the southern Sierra Nevada (Knapp, personal observations), and it is possible that at least the subadults of *B. canorus* are also palatable. Second, assuming that predators must learn to reject unpalatable toad and newt life stages (Peterson and Blaustein, 1991), some mortality of *B. canorus* and *T. t. sierrae* may be incurred as a result of handling by trout during this learning process. The extent to which such mortality might influence population densities of these two species remains unknown.

The species-specific habitat associations suggested by the regression models are largely self-explanatory. However, I provide a brief discussion of these associations for *B. canorus* and *R. muscosa*, as this information may be particularly relevant for future management efforts directed at these two declining species. For *B. canorus*, the probability of occurrence was strongly associated with shoreline substrate composition and elevation, with site occupancy being highest at sites with shorelines dominated by meadow vegetation and at sites located at elevations above 2800 m. These findings generally support the existing qualitative descriptions of habitat use by *B. canorus*, and together suggest that *B. canorus* is found at sites ranging widely in water depth but is strongly associated with aquatic habitats located in meadows, particularly those meadows found in the subalpine and alpine zones (Grinnell and Storer, 1924; Mullally, 1953; Karlstrom, 1962). This close association by *B. canorus* with meadow habitats suggests that any management activities undertaken in meadows that lie within the range of *B. canorus* should be implemented in such a way as to eliminate negative impacts on this declining species.

The presence of *R. muscosa* in Yosemite was positively associated with water depth, amount of meadow vegetation on the shoreline, and elevation. The response curve for water depth was remarkably similar in shape to that for *R. muscosa* in the southern Sierra Nevada (Knapp et al., 2003). Both suggest that the probability of occurrence by *R. muscosa* increases sharply between 0 and 4–5 m and remains high for depths >5 m. The affinity by *R. muscosa* for relatively deep water bodies is likely a consequence of the fact that larvae require two or more years to reach metamorphosis, thereby generally restricting successful breeding to water bodies that do not dry or freeze completely (Bradford, 1989; Knapp et al., 2003). Superficially, the association between *R. muscosa* presence/absence and elevation was markedly different between Yosemite and the southern Sierra Nevada. Although elevation was a significant predictor of *R. muscosa* occurrence in both studies, the probability of occurrence was an increasing function of elevation in Yosemite and it was a decreasing function of elevation in the southern Sierra Nevada (Knapp et al., 2003). This difference in the effect of elevation is likely the result of each study only sampling a portion of the elevational range occupied by *R. muscosa*. Sampled water bodies in Yosemite National Park ranged in elevation from 1079 to 3615 m, and the response curve showed a linear increase in p_i from the lowest elevations up to approximately 2800 m, after which it remained constant up to the highest elevations. In the southern Sierra Nevada, sampled water bodies spanned a much narrower range of elevations (2932–3749 m) and the probability of occurrence was relatively constant from 2900 to 3500 m, and then dropped sharply between 3500 and 3750 m (Knapp et al., 2003). When viewed together, however, these data suggest that the probability of occurrence for *R. muscosa* in the Sierra Nevada increases from 1500 to approximately 2800 m, remains high and relatively constant from 2800 to 3500 m, and then decreases abruptly as elevation approaches the known upper elevational limit for *R. muscosa* of 3650 m (Mullally and Cunningham, 1956; Stebbins, 1985).

5.2. Reptiles

The distributions of the garter snakes, *T. c. couchi* and *T. e. elegans*, were strongly associated with the distributions of their amphibian prey, supporting the results of previous studies that also reported strong associations between *T. elegans* and amphibians (Arnold and Wassersug, 1978; Jennings et al., 1992; Matthews et al., 2002). Presence/absence of *T. e. elegans* was strongly influenced by the presence/absence of *H. regilla* and *R. muscosa*, but not by *B. canorus* or *T. t. sierrae*. Given that the distributions of *H. regilla* and *R. muscosa* are both negatively affected by the presence of nonnative trout (Knapp and Matthews, 2000; Matthews et al., 2002; this study), trout are likely having an indirect negative effect on *T. e. elegans* mediated through their shared amphibian prey. The similar life histories of *T. e. elegans* and *T. c. couchi* suggests that the same mechanism may underlie the negative association between trout presence/absence and *T. c. couchi*. The lack of a significant association between *T. e. elegans* and either *B. canorus* or *T. t. sierrae* suggests that either this snake is actively avoiding these prey species or that the number of sites inhabited by *B. canorus* or *T. t. sierrae* in Yosemite was too small to allow detection of a significant association.

In addition to the positive association between amphibian presence and the probability of occurrence for both garter snake species, the presence of trout had a negative effect on snake occurrence (highly significant for *T. e. elegans*, marginally nonsignificant for *T. c. couchi*). This effect of trout on garter snake presence/absence is unlikely to be the result of direct predation by trout on garter snakes given the large size of even recently born garter snakes relative to the size of most trout (Matthews et al., 2002). In addition, snakes were never found in the stomachs of trout captured during the current study. The significant effect of trout on garter snake occurrence may instead be a result of trout predation reducing not only the probability of occurrence by amphibians but also amphibian densities (Knapp and Matthews, 2000; Knapp et al., 2001; Matthews et al., 2002). These lower amphibian densities may in turn result in a lower probability of occurrence for garter snakes.

Further research will be necessary to determine whether the extirpation of amphibian populations by trout predation is causing landscape-scale declines of these two garter snakes (Matthews et al., 2002) or whether the snakes are instead switching their foraging from lentic to terrestrial habitats. The fact that garter snakes were never found away from water during the hundreds of kilometers traversed by field crews while conducting surveys suggests that the latter possibility may be unlikely.

5.3. Implications for conservation

The far-reaching negative impacts of nonnative trout on the herpetofauna of lakes in Yosemite National Park documented in the current study suggests the importance of removing trout from as many sites in the Park as possible. The available literature suggests that at least *R. muscosa* may be able to recover following trout disappearance (Knapp et al., 2001), and ongoing trout removal efforts in the southern Sierra Nevada (using the methods described in Knapp and Matthews (1998)) have resulted in rapid increases in *R. muscosa* population densities (Vredenburg, 2004; Knapp, unpublished data). However, nonnative trout are not the only stressor currently impacting herpetofauna in Yosemite National Park. The possibility that airborne agricultural contaminants are negatively affecting amphibians was suggested by Davidson et al. (2002), who provided evidence that sites in the Sierra Nevada where amphibians have gone extinct have greater amounts of agricultural land upwind (a proxy for the intensity of pesticide use) than do sites where amphibians are extant. In addition, a recently described chytrid fungus (*Batrachochytrium dendrobatidis* ; Berger et al., 1998; Fellers et al., 2001) is increasingly being associated with the extinction of amphibian populations both in the Sierra Nevada (Green and Kagarise Sherman, 2001; Knapp, unpublished data) and around the world (Lips, 1998, 1999; Muths et al., 2003). Given that multiple stressors are likely influencing the persistence of Sierra Nevada amphibian populations, long-term studies will be necessary to determine whether fish eradication alone is sufficient to restore Yosemite's lake-dwelling herpetofauna.

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