available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/biocon

Evidence of indirect impacts of introduced trout on native amphibians via facilitation of a shared predator

Karen L. Pope[a,b,*], *Justin M. Garwood*[a,c], *Hartwell H. Welsh Jr.*[a], *Sharon P. Lawler*[b]

[a]*USDA Forest Service, Pacific Southwest Research Station, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA 95521, USA*
[b]*UC Davis, One Shields Avenue, Davis, CA 95616, USA*
[c]*Department of Wildlife Management, Humboldt State University, Arcata, CA 95521, USA*

ARTICLE INFO

Article history:
Received 7 June 2007
Received in revised form
7 March 2008
Accepted 11 March 2008
Available online 16 May 2008

Keywords:
Hyperpredation
Indirect effects
Amphibian declines
Predator-prey interaction
Non-native
Invasive species

ABSTRACT

Hyperpredation occurs when non-native prey facilitate invasive predators, which then suppress native prey. Direct impacts of introduced fish on amphibians are well studied, but the role of fish in supporting shared predators has not been considered. We present evidence for indirect effects of trout on amphibians through snake predation. Analyses of the diet, distribution and density of the Pacific coast aquatic garter snake (*Thamnophis atratus*) relative to the sympatric common garter snake (*Thamnophis sirtalis*) in the Klamath Mountains of California suggest that trout introductions facilitated expansion of *T. atratus* by providing alternative prey. *T. atratus* diet included trout and amphibians whereas *T. sirtalis* preyed solely upon amphibians. The distribution and density of *T. atratus* matched that of introduced trout instead of native amphibians. Populations of *T. atratus* could reach high densities in the absence of high densities of amphibians. When the snakes opportunistically prey upon amphibians whose numbers are already directly impacted by trout, they can cause significant additional declines. When *T. atratus* was present in lake basins, native Cascades frogs (*Rana cascadae*) were rarer than in basins without *T. atratus*. This case differs from other hyperpredation studies because the two prey species also interact via intraguild predation. Given the worldwide practice of stocking fish into aquatic habitats, it is important to understand the consequences of the practice on food-web structure and ecosystem functioning. Bottom-up impacts of introduced predators should be considered as well as top-down so that managers can incorporate the range of ecosystem-level effects into conservation goals and decisions.

1. Introduction

A predator's impact on prey abundance can range from inconsequential (e.g., Cardona, 2006) to severe (e.g., Halpern et al., 2006). Strong top-down effects often occur when alternate prey sources support increased densities of generalist predators, which then depress local prey populations (Polis et al., 1997; Sinclair et al., 1998). When the renewal rate of alternate prey is high then predators are assured a food supply they cannot overexploit. As a consequence, predator success becomes decoupled from local consumer-resource dynamics (Schoener and Spiller, 1996; Polis et al., 1997). This form of apparent competition (Holt, 1977) or indirect amensalism (Chaneton and Bonsall, 2000) is known for several systems.

* *Corresponding author:* Address: USDA Forest Service, Pacific Southwest Research Station, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA 95521, USA. Tel.: +1 707 825 2957; fax: +1 707 825 2901.
E-mail addresses: kpope@fs.fed.us (K.L. Pope), justingarwood@gmail.com (J.M. Garwood), hwelsh@fs.fed.us (H.H. Welsh), splawler@ucdavis.edu (S.P. Lawler).
0006-3207/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2008.03.008

For example, deep-sea fishes periodically migrate into shallow waters where they provide an alternate prey for sea otters, which then depress local sea urchin populations (Watt et al., 2000). Apparent competition can also be induced by humans in the form of introduced species. For example, the introduction of feral pigs to the California Channel Islands has sustained an unnaturally large population of predatory golden eagles. Golden eagles also prey upon the endemic island fox, reducing its numbers to near extinction (Roemer et al., 2002).

The ecological importance of facilitation of predators by non-indigenous prey and the resulting indirect effects have only recently been highlighted (Noonburg and Byers, 2005; Rodriguez, 2006). "Hyperpredation" refers to the indirect interactions between non-indigenous and native prey via a shared predator (Smith and Quin, 1996; Courchamp et al., 1999) and occurs when a non-indigenous prey species indirectly facilitates the decline of a native prey species by enabling a shared predator to increase in abundance (Smith and Quin, 1996). The shared predator often moves into the habitat of the indigenous prey by following the expansion of the non-indigenous prey (Courchamp et al., 2000).

Most studies on introduced predatory species focus on their direct effects on native biota. For example, the direct negative effects of introduced fish on native amphibian distribution and abundance in mountain lakes have been studied extensively (e.g., Vredenburg, 2004; Welsh et al., 2006; Knapp et al., 2007). Additional studies have found top-down cascading indirect effects due to fish introductions (Scavia et al., 1986; Knapp et al., 2001; Schindler et al., 2001). All of these studies consider trout only as predators.

We take an alternate approach and focus on introduced trout as a supplemental prey source that facilitates the increase and spread of the Pacific coast aquatic garter snake (*Thamnophis atratus*), a species that preys on both fishes and amphibians (Lind and Welsh, 1994). The introduction of a common, supplemented (via stocking) prey source in mountain lakes of northern California may have allowed *T. atratus* to expand its range upslope from its more typical lower elevation stream habitats (Rossman et al., 1996; Fitch, 1984) into these historically fishless lentic habitats. In this region, steep canyon gradients created during Pleistocene glaciations prevented colonization by fishes into lakes higher than 1500 m in elevation (Welsh et al., 2006). Beginning in the 1800 s, various salmonids (primarily *Oncorhynchus*, *Salmo*, and *Salvelinus* spp., hereafter "trout") were introduced to lakes for recreation and stocking continues today. We hypothesize that there are indirect consequences of introduced trout in the high elevations of the Klamath Mountains of northern California by means of increased predation on the Cascades frog (*Rana cascadae*) by *T. atratus*. *R. cascadae* is a native lentic breeding amphibian in high elevations of the Klamath Mountains and is a known prey item of introduced trout (Simons, 1998) and garter snakes (Garwood and Welsh, 2005).

This study expands on previous studies of hyperpredation (Smith and Quin, 1996; Courchamp et al., 2000; Roemer et al., 2002; Kristan and Boarman, 2003) by including two prey species that also interact via intraguild predation (when species pairs have both competitive and predator/prey interactions; Polis et al., 1989). *R. cascadae* may be especially sensitive to hyperpredation by *T. atratus* because it already has depressed population numbers due to trout (Welsh et al., 2006). In addition, the frog requires at least semi-permanent water throughout its life, making all life stages vulnerable to aquatic garter snake predation.

We evaluate the hyperpredation hypothesis by comparing the diet, distribution, and density of the facilitated predator (*T. atratus*) with another native garter snake species, the common garter snake (*Thamnophis sirtalis*). Although *T. sirtalis* occurs in a wide range of habitats and has a broad prey base range-wide, it has been found to be a local amphibian specialist in high elevation lentic habitats (Kephart, 1982). Based on existing literature, we predicted that the diet of *T. sirtalis* in the Klamath Mountains would consist primarily of amphibians (Kephart, 1982; Rossman et al., 1996), while the diet of *T. atratus* would consist of both introduced trout and amphibians (Lind and Welsh, 1994). By eating trout as well as native prey, *T. atratus* populations would be able to succeed regardless of native prey densities. In contrast to *T. sirtalis*, the distribution and densities of *T. atratus*, therefore, should not be strongly related to densities of native prey. Where *R. cascadae* co-occur with trout, the additional predation pressure by *T. atratus* could be detrimental to *R. cascadae* populations. We assess the potential impacts to *R. cascadae* by comparing the relative density of frogs in trout-containing basins with and without additional predation by *T. atratus*.

2. Materials and methods

We make use of three datasets collected from the Klamath Mountains between 1999 and 2006: the first is a large-scale snapshot census of lentic habitats throughout three wilderness areas (landscape survey), the second involves repeated sampling of 16 Trinity Alps Wilderness headwater basins over four years (basin study), and the third is a detailed case study in one sub-watershed consisting of a lake, several permanent ponds, and a complex wet meadow system systematically sampled for four years (case study, Fig. 1). The combination of datasets allows us to compare patterns across spatial scales and with different levels of detail.

2.1. *Landscape survey*

The main goal of the landscape survey was to document distributions and relative abundances of introduced trout, amphibians and garter snakes throughout the lentic water bodies (lakes, ponds, and wet meadows) of the Trinity Alps, Marble Mountains, and Russian wilderness areas (Welsh et al., 2006). All three of these wilderness areas are within the range and habitat of *R. cascadae*. Until recently, approximately 90% of lakes greater than 1 ha in these wildernesses were stocked with trout on an annual or biennial basis. Since 2002, the California Department of Fish and Game (CDFG) suspended stocking in approximately half of the lakes to assess the impacts and sustainability of introduced trout.

During the summers of 1999–2002, we surveyed 728 water bodies between 1525 and 2290 m in elevation, mostly within sub-alpine habitats. Because of the high number of water bodies and their remoteness, each site was sampled only once. The presence or absence and estimated density of trout

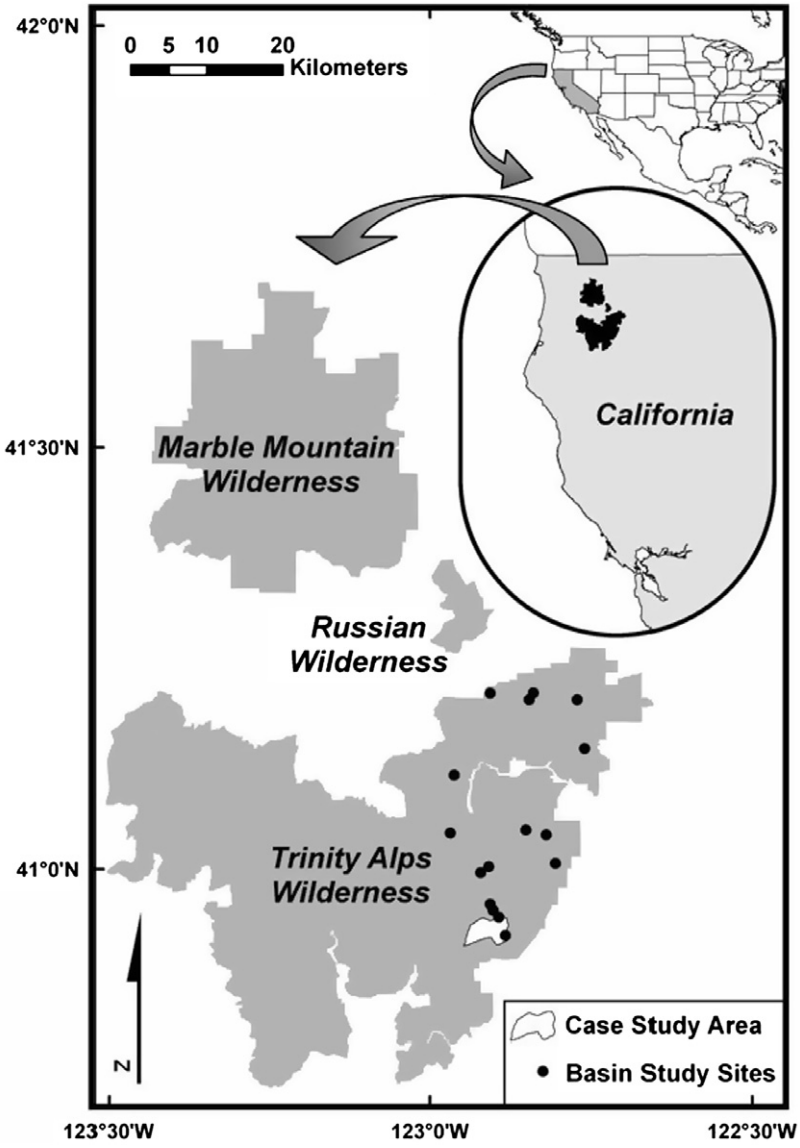

Fig. 1 – Map of the study area. Lentic habitats in the three wilderness areas were surveyed in the landscape survey. Study basins sampled in the basin and case studies are identified.

were determined by a timed gill-net set at each water body deep enough to support trout (Welsh et al., 2006). Captured trout were identified and counted. In the Sierra Nevada, repeated gill-net sets indicated that single net sets were close to 100% accurate in determining fish presence or absence (Knapp and Matthews, 2000).

To determine presence and relative numbers of amphibians and garter snakes, we used a visual encounter survey (VES; Crump and Scott, 1994). We searched the shoreline and littoral habitats, looking under banks and logs and in the substrates. Amphibians and snakes were identified to species and counted by life stage. Five species of amphibians were encountered regularly including *R. cascadae*, *Pseudacris regilla* (Pacific treefrog), *Bufo boreas* (western toad), *Ambystoma macrodactylum* (long-toed salamander) and *Taricha granulosa* (rough-skinned newt). *T. atratus* and *T. sirtalis* were the only snakes consistently found.

2.2. *Basin study*

In 2003–2006, we sampled garter snake diet and density in 16 Trinity Alps lake basins (1920–2210 m in elevation) as part of a study assessing the impacts of introduced trout on native fauna (Fig. 1). Lakes sampled included four that were naturally fishless, four where trout were removed in September 2003 through June 2004, four where trout stocking was suspended in 2002, and four that were stocked annually. Garter snakes were surveyed five to six times per summer at two-week intervals in each basin via capture–mark–recapture surveys. Lake, pond, wet meadow and stream edges up to 50 m upstream and downstream of lakes were systematically searched for garter snakes. Captured adult snakes (>340 mm SVL) were individually marked using passive integrated transponders (PIT tags). In 2005 and 2006, all garter snakes caught were palpated to force regurgitation of food in their digestive

tracts as described by Fitch (1987). We recorded the species and life stage of stomach contents.

2.3. Case study

The case study was incorporated to provide local-scale detail on the distribution of the garter snakes in relation to *R. cascadae* and trout, as well as to add to the garter snake diet information. From 2003 to 2006, we conducted mark-recapture surveys on garter snakes and post-metamorphic *R. cascadae* in the headwaters of Deep Creek, a 342 ha glacial cirque (1960–2279 m in elevation) in the Trinity Alps Wilderness (Fig. 1). Habitats within the basin include one lake, two large semi-permanent ponds and a mosaic of 12 meadow patches, which collectively contain hundreds of small ponds and stream segments. All captured garter snakes were palpated and stomach contents were identified. Approximately 10 basin-wide surveys were conducted per year and spanned the entire active period of these animals (May–October). Adult snakes were marked with PIT tags and snakes $\leqslant$340 mm were marked by ventral scale-clipping similar to Brown and Parker (1976). Aquatic habitats and locations of all snakes and *R. cascadae* were recorded using a global positioning system (GPS, Trimble GeoExplorer III®, Sunnyvale, California). Fish distribution and density were determined by a bounded snorkel count within all permanent streams (Hankin and Reeves, 1988). Three counts were conducted in each habitat unit (riffle, run, pool) by three different divers with 15 min of inactivity between each count.

3. Analysis

3.1. Diet

For the diet analysis of *T. atratus* and *T. sirtalis*, we combined data from the basin and case studies after ensuring that no significant differences existed between the studies in types of food (trout versus amphibians) found in either species' stomachs. We found only amphibians in all *T. sirtalis* stomachs so did not run statistical comparisons between studies and found no difference for *T. atratus* (Yates' chi-square test, df = 1, $P = 0.5$).

We constructed cumulative prey curves (Hurtubia, 1973) for *T. atratus* and *T. sirlatis* to ensure that our sample sizes were sufficient to describe the diet of each species in the Trinity Alps. We used only one stomach sample per individual per year. Prey types were categorized by species and life stage (larvae, juvenile, adult). We plotted the cumulative number of prey types against the number of randomly selected stomach samples. Starting with 50% of the samples, we calculated linear and exponential regression equations and compared the goodness of fit coefficients (R^2) for the line and exponential curve. If the R^2 for the exponential curve was higher than the R^2 for the linear relation then the sample size was considered sufficient (Castriota et al., 2005). If the fit of the linear relation was higher then we included 75% of the samples and reran the comparisons.

We tested whether the proportion of snakes with prey in their stomachs differed between species and if the proportion of amphibian or fish prey differed by species using Yates' chi-square tests. We also tested whether the garter snakes differentially hunted fully aquatic (trout or amphibian larvae) or semi-terrestrial (amphibian juveniles and adults) prey. *P*-values were adjusted using the Bonferroni correction for multiple tests. Differential digestion among prey types was unlikely to have created a bias in observed prey ratios because most of the stomach contents (94%) were barely digested and easily identifiable to species. The good condition of stomach contents indicated that we captured garter snakes when they were actively feeding. Tracking data from eight radio-transmittered frogs that were eaten by garter snakes showed that once their stomachs were full, the snakes moved to protected upland resting areas to digest their food (Garwood, unpublished data).

3.2. Distribution

Using VES presence/undetected data from the landscape survey, we compared the distribution of *T. atratus* and *T. sirtalis* to the distribution of prey (introduced trout and native amphibians), distribution of the other snake species, site habitat variables, and site location variables. Our goal was to determine if garter snake distributions were related to the distribution of either or both of the prey types while controlling for garter snake species interactions and differences in habitats and spatial autocorrelation (Hobert et al., 1997). We used generalized additive models for the analyses (Hastie and Tibshirani, 1991; see also Knapp, 2005). Prior to analyses, we tested for multicollinearity among predictor variables by calculating the condition number (sqrt(max. eigenvalue/min. eigenvalue)) of the variance–covariance matrix of all covariates. The condition number equaled 4.29, much less than the cutoff of 30 for severe collinearity (Belsley et al., 1980).

We modeled the probability (p) of finding each snake species at location i as

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

where the linear predictor θ is the following function of the covariates:

$$\theta = \text{Fish} + \text{Snake} + \text{Amphibians} + \text{Wilderness} + \text{lo(Perimeter)} + \text{lo(Elevation)} + \text{lo(Location)}.$$

Fish, Snake, and Amphibians are categorical variables indicating presence/non-detection of fish, the other species of garter snake and amphibians during VES. Wilderness is a categorical variable representing the wilderness area that the water body occurs in or near (Welsh et al., 2006). lo(·) is a nonparametric loess smoothing function that characterizes the relationship of the continuous variables on p_i. The variable lo(Perimeter) is an estimate of the length of the shoreline of the water body and lo(Location) is a smooth surface of UTM northing and easting.

To evaluate predictor variables we calculated the change in deviance resulting from dropping each variable while retaining all others ("residual" deviance). We used analysis of deviance and likelihood ratio tests to test the significance of each of the predictor variables. To provide a standardized estimate of the influence of each variable in the models, we calculated the percent increase in deviance due to omission of each

variable. Given the relatively large sample size ($n = 728$) used in the regression models, predictor variables could show statistical significance even with weak associations with snake presence. Therefore, predictor variables were considered to have significant effects only when $P \leqslant 0.01$. Regression analyses were calculated using S-Plus (S-Plus, 2001).

At the local-scale, we mapped the specific locations of all *T. atratus* and *T. sirtalis* found in the case study. We calculated 100% fixed kernel utilization distribution (UD) estimates (bandwidth: 100) for each species using Hawth's Analysis extension (Beyer, 2004) in a geographic information system (GIS, ArcGIS 9.0®). A kernel UD estimator produces a nonparametric distribution representing the likelihood of finding an animal and the intensity of use by that animal at any particular location (Worton, 1989; Marzluff et al., 2004). Although kernel estimates are most commonly used to approximate an individual animal's home range (Worton, 1989; Millspaugh et al., 2006), we applied them here to all located individuals of a species to visually relate the species' UD to prey distribution. We included only the initial observation of an individual per year to remove spatial dependence related to multiple locations of the same individual (*T. atratus*: $n = 69$, *T. sirtalis*: $n = 87$). To quantify the spatial association of garter snakes and prey, we mapped *R. cascadae* and trout locations in the basin. For *R. cascadae* we used the same UD analysis as used for the snakes. Utilization distributions were not calculated for trout because trout distributions could be more accurately displayed using a bar graph given that they were found only in a short stream segment with distinct physical barriers. We used 2×2 contingency tables to compare the overlap of the 95% distribution kernels of the garter snake species with the distributions of the prey. For this analysis we used 95% kernels instead of 100% to better restrict the distribution fit closer to the actual core use areas (Millspaugh et al., 2006). The Bonferroni correction was applied for multiple comparisons.

We could not use the basin study for statistical comparisons of the garter snake species in lakes with and without fish because we only found *T. atratus* in three of the 16 lakes. One of the lakes was a fish removal lake where we found *T. atratus* in 2003 prior to fish removals and not again in the following three years after fish removal.

3.3. Density

To estimate *T. atratus* and *T. sirtalis* densities, we used 2005–2006 mark-recapture data from two basins in the basin study. We estimated capture probabilities and population sizes using Jolly–Seber capture–recapture models in the program JOLLY ("robust design"; Pollock et al., 1990). This design includes several secondary sampling occasions within each primary sampling period (year) and allows for time-specific changes in parameters such as population size and survival. We encountered *T. atratus* at two additional basins and *T. sirtalis* at 13 additional basins but did not capture enough snakes to compute population estimates.

We then used VES data from the landscape study in Poisson regressions to test if *T. atratus* and *T. sirtalis* relative abundances at sites were related to prey type. We compared the relative number of snakes found at a site with the relative abundance of amphibians and density of trout, while controlling for presence of the other snake species, water body perimeter, elevation, wilderness area, and location. Trout densities were estimated as catch per unit effort (CPUE: number of fish captured per hour of net set). A linear regression comparing CPUE to actual density of fish in four lakes in the basin study where fish were completely removed showed that CPUE and density are highly correlated ($r^2 = 0.95$, P-value < 0.01).

Finally, we tested the hypothesis that *T. atratus* negatively impacts populations of *R. cascadae*. We created a sub-basin variable from the landscape data using GIS to link all unique sites within the same watershed that were within 500 m of each other. We chose 500 m because Welsh and Lind (unpublished data) found that about 90% of marked *T. atratus* moved less than 500 m during a 15 year movement study. Using only sub-basins with trout present in at least one water body ($N = 245$), we calculated the total number of *R. cascadae* observed in the sub-basin. We compared the relative abundance of *R. cascadae* in sub-basins with and without *T. atratus* using both a univariate Wilcoxon signed-rank test and Poisson regression to control for the number of water bodies in the sub-basin given that a diversity of water bodies in a sub-basin may positively influence the number of *R. cascadae* in the sub-basin (Welsh et al., 2006).

4. Results

4.1. Diet

Diet composition differed between the snake species: *T. atratus* preyed on both fish and amphibians whereas *T. sirtalis* preyed solely on amphibians ($X^2_1 = 55.9$, $P < 0.0001$, Fig. 2). In 54 *T. atratus* stomachs with food, we found three species of amphibians and two species of trout, while in 90 *T. sirtalis* we found five species of amphibians (Fig. 2). *R. cascadae* were in 33% of the *T. atratus* stomachs with food and in 66% of the *T.*

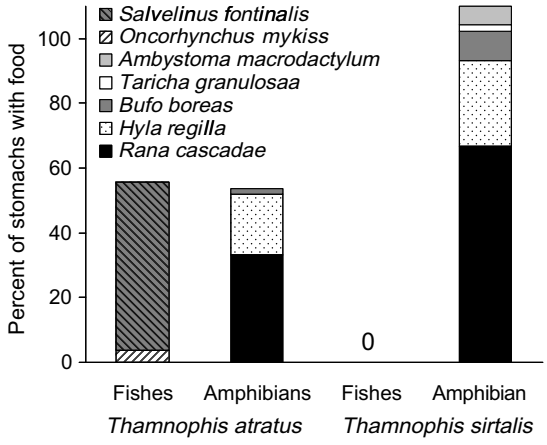

Fig. 2 – Percent of *T. atratus* and *T. sirtalis* with fishes or amphibians in their stomachs. Prey types are distinguished by species. The two fish species are represented by striped bars. For both species, the combined percent of prey is greater than 100 because some snakes had more than one species in their stomachs.

sirtalis. There was an interspecific difference in proportion of aquatic versus semi-terrestrial prey ($X_1^2 = 19.9$, $P = 0.05$) with 92% of *T. atratus* containing fully aquatic prey (amphibian larvae or fish), compared to 58% of *T. sirtalis*. Of amphibian prey, the larval life stage was the most commonly eaten for both *T. atratus* (73%) and *T. sirtalis* (57%). The proportion of snakes with prey in their stomachs did not differ between species (*T. atratus* = 36%, *T. sirtalis* = 31%, $X_1^2 = 0.8$, $P = 0.37$). Sample sizes were sufficient to describe diets of both garter snake species in the Trinity Alps Wilderness. Cumulative prey curves were a better fit with an exponential curve ($R^2 = 0.93$) than a linear relation ($R^2 = 0.71$) using just 75% of *T. atratus* stomach samples (df = 39) and 50% of *T. sirtalis* samples (df = 46, exponential $R^2 = 0.97$, linear $R^2 = 0.71$).

4.2. Distribution

In the landscape survey, *T. atratus* were found more often at sites where trout were present ($X_1^2 = 77.1$, $P < 0.0001$) but were not associated with amphibian presence ($X_1^2 = 0.7$, $P = 0.8$). In contrast, *T. sirtalis* were found more often where amphibians were present ($X_1^2 = 37.9$, $P < 0.0001$) but were not associated

Table 1 – Change in deviance and statistical significance of predictor variables used in the binomial generalized additive models developed for T. atratus and T. sirtalis distributions

Parameter	*Thamnophis atratus*		*Thamnophis sirtalis*	
	Deviance increase[a]	P-value	Deviance increase[a]	P-value
Salmonid presence	33 (31.4)	<0.001	0.1 (0.1)	0.76
Amphibian presence	0.2 (0.2)	0.63	60 (54.1)	<0.001
Perimeter	3 (2.9)	0.3	11 (9.9)	0.01
Elevation	5 (4.8)	0.34	10 (9.0)	0.05
Wilderness area	0.5 (0.5)	0.79	5 (4.5)	0.09
UTMs	10 (9.5)	0.18	17 (15.3)	0.02

a Deviance increase: increase in deviance resulting from dropping the selected variable from the model. The percentage increase in deviance is given in parentheses, and was calculated as (deviance increase/(null deviance-model deviance)) × 100 (Knapp, 2005). Null deviance was 348 (df = 727) for *T. atratus* and 713 (df = 727) for *T. sirtalis*. Model (residual) deviance was 243 (df = 709) for *T. atratus* and 602 (df = 709) for *T. sirtalis*.

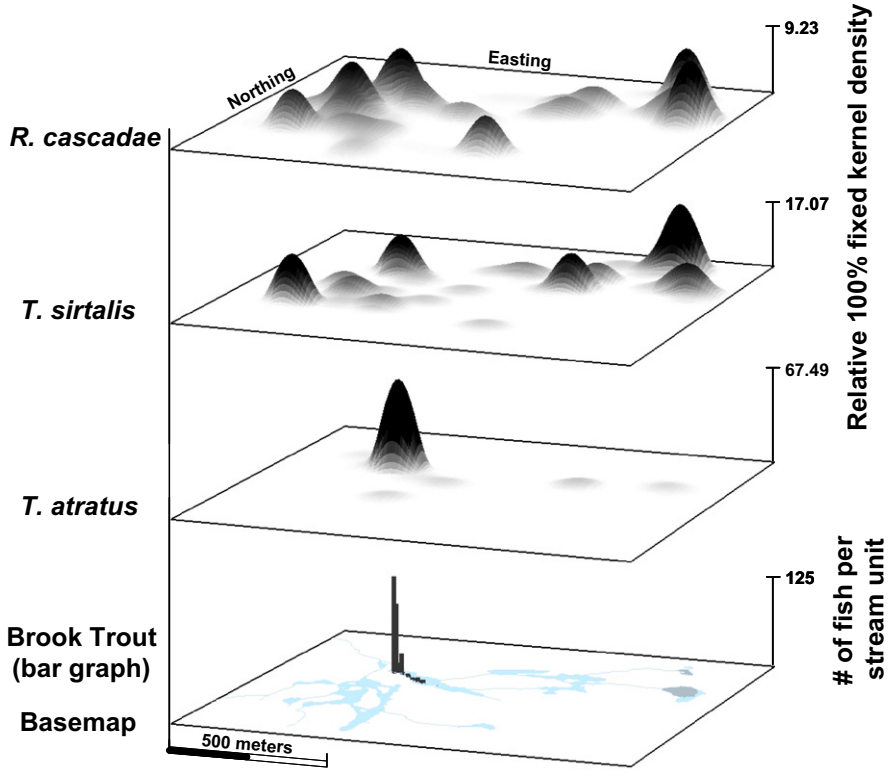

Fig. 3 – Fixed-kernel utilization distributions (bandwidth = 100) for *R. cascadae* (*n* = 5656), *T. sirtalis* (*n* = 87), and *T. atratus* (*n* = 69) locations within Deep Creek Basin, Trinity Alps Wilderness. The height of the density function depicts the relative probability of an individual occurring at each location within the study area. Relative kernel heights are estimated independently for each species and are not comparable across species. The bottom panel shows aquatic habitats within Deep Creek Basin and includes a spatially related bar graph representing estimated densities of trout (*n* = 348) in the basin.

Table 2 – Change in deviance and statistical significance of predictor variables used in the Poisson generalized additive models developed for correlating relative abundances of T. atratus and T. sirtalis with predictor variables

Parameter	*Thamnophis atratus*		*Thamnophis sirtalis*	
	Deviance increase[a]	*P*-value	Deviance increase[a]	*P*-value
CPUE	146.5 (21.0)	<0.001	1.3 (1.7)	0.53
T. atratus presence			6.6 (9.0)	0.01
T. sirtalis presence	33.8 (4.8)	0.01		
Amphibians	65.6 (9.4)	0.003	39.8 (54.5)	<0.001
Perimeter	94.5 (13.6)	0.001	10.3 (14.1)	0.007
Elevation	11.9 (1.7)	0.22	8.7 (11.9)	0.009
Wilderness area	69.5 (10.0)	0.007	14.1 (19.3)	0.007
UTMs	48.5 (6.9)	0.01	3.2 (4.4)	0.12

a Deviance increase: increase in deviance resulting from dropping the selected variable from the model. The percentage increase in deviance is given in parentheses, and was calculated as (deviance increase/(null deviance-model deviance)) × 100 (Knapp, 2005). Null deviance was 987 (df = 727) for *T. atratus* and 209 (df = 727) for *T. sirtalis*. Model (residual) deviance was 290 (df = 697) for *T. atratus* and 136 (df = 697) for *T. sirtalis*.

with trout ($X_1^2 = 0.0$, $P = 1.0$). 162 *T. atratus* were detected at 51 of 728 water bodies (7%) and 286 *T. sirtalis* were detected at 140 water bodies (19%). In binomial generalized additive modeling, *T. atratus* showed a strong positive relationship with the occurrence of introduced trout, but no relationship with native amphibians after controlling for habitat and spatial influences (Table 1). *T. atratus* was also negatively associated with presence of *T. sirtalis*. None of the habitat covariates influenced the occurrence of *T. atratus* (Table 1). Conversely, modeling results for *T. sirtalis* showed a strong positive relationship with the occurrence of amphibians but no relationship with introduced trout (Table 1). Presence of *T. atratus*, size of the water body, and site location also predicted *T. sirtalis* occurrence (Table 1).

The case study showed compelling correlations between each snake species and its main prey in the distribution maps for the garter snakes, trout, and *R. cascadae* (Fig. 3). Sixty three percent of the distribution kernel for *T. atratus* encompassed the trout-containing habitat compared to 11% of the distribution kernel for *T. sirtalis* ($X^2 = 48.9$, $P < 0.0001$). Moreover, only 23% of the kernel for *T. atratus* overlapped with the kernel for *R. cascadae* compared to 63% of the kernel for *T. sirtalis* ($X^2 = 24.8$, $P < 0.0001$).

4.3. *Density*

In the landscape survey, we found greater numbers of *T. atratus* than *T. sirtalis* when garter snakes were found at a site ($Z = 2.3$, $P = 0.02$), with 3.4 ± 0.51 (mean ± SE) *T. atratus* compared to 2.0 ± 0.14 *T. sirtalis*. Similarly, in the basin study, *T. atratus* attained approximately twice the density of *T. sirtalis* at the basins where each was sufficiently abundant for mark-recapture estimates. *T. atratus* had an average adult density of ~7 snakes/ha at Ward Lake (3.83 ha) over two sampling years (mean population = 29, range: 15 ± 4.8–44 ± 17.6, capture probability: 0.13 ± 0.04). *T. sirtalis* had an average density of ~3 adults/ha at Hidden Lake (4.17 ha) (mean population = 13, range: 8 ± 3.1–28 ± 7.7, capture probability: 0.23 ± 0.06).

Relative abundance of *T. atratus* was strongly correlated with trout density, after controlling for habitat and spatial covariates (Table 2, Fig. 4A). A positive relationship was also found between *T. atratus* and relative abundance of amphibians, absence of *T. sirtalis*, and size of the water body (Table 2, Fig. 4A). Other significant predictor variables included wilderness area and UTMs (Table 2, Fig. 4A). The relative abundance of *T. sirtalis* found at a site was positively correlated with relative abundance of amphibians but there was no relationship found with trout density (Table 2, Fig. 4B). Other significant predictor variables included presence of *T. atratus*, wilderness area, water body perimeter, and elevation (Table 2, Fig. 4B). The location covariate (UTMs) was not presented graphically because its complexity is difficult to interpret and provides no visual insight into the relationship between the garter snakes and their prey.

We found fewer *R. cascadae* in trout-containing sub-basins where we also found *T. atratus* ($n = 19$, mean = 54, SE = 16) compared to trout-containing sub-basins where we did not find *T. atratus* ($n = 207$, mean = 83, SE = 24), and this difference was marginally significant ($Z = 1.6$, $P = 0.06$). Multiple regression results showed a significant negative relationship between relative abundance of *R. cascadae* and presence of *T. atratus* after controlling for number of water bodies in the sub-basin (*T*-value = −2.6, df = 221, $P = 0.001$).

5. Discussion

This study provides strong correlative evidence that the introduction of trout has facilitated populations of *T. atratus* in high elevation wilderness lake basins of the Klamath Mountains, based on our analyses of the diet, distribution and density of *T. atratus* relative to *T. sirtalis*. The distribution and density of *T. atratus* follows the distribution and density of introduced trout instead of native amphibian prey, which they also opportunistically eat. Populations of *T. atratus* are not reliant on native prey populations and, thus, can reach high densities in the absence of high densities of amphibians. When the snakes opportunistically prey upon native amphibians whose numbers may already be directly impacted by trout (Welsh et al., 2006), they can cause significant additional declines (Noonburg and Byers, 2005). We found *R. cascadae* in approximately 33% of the *T. atratus* stomachs that contained food. A negative impact of *T. atratus* on *R. cascadae* is suggested by the finding that *R. cascadae* was less abundant in sub-basins with versus without

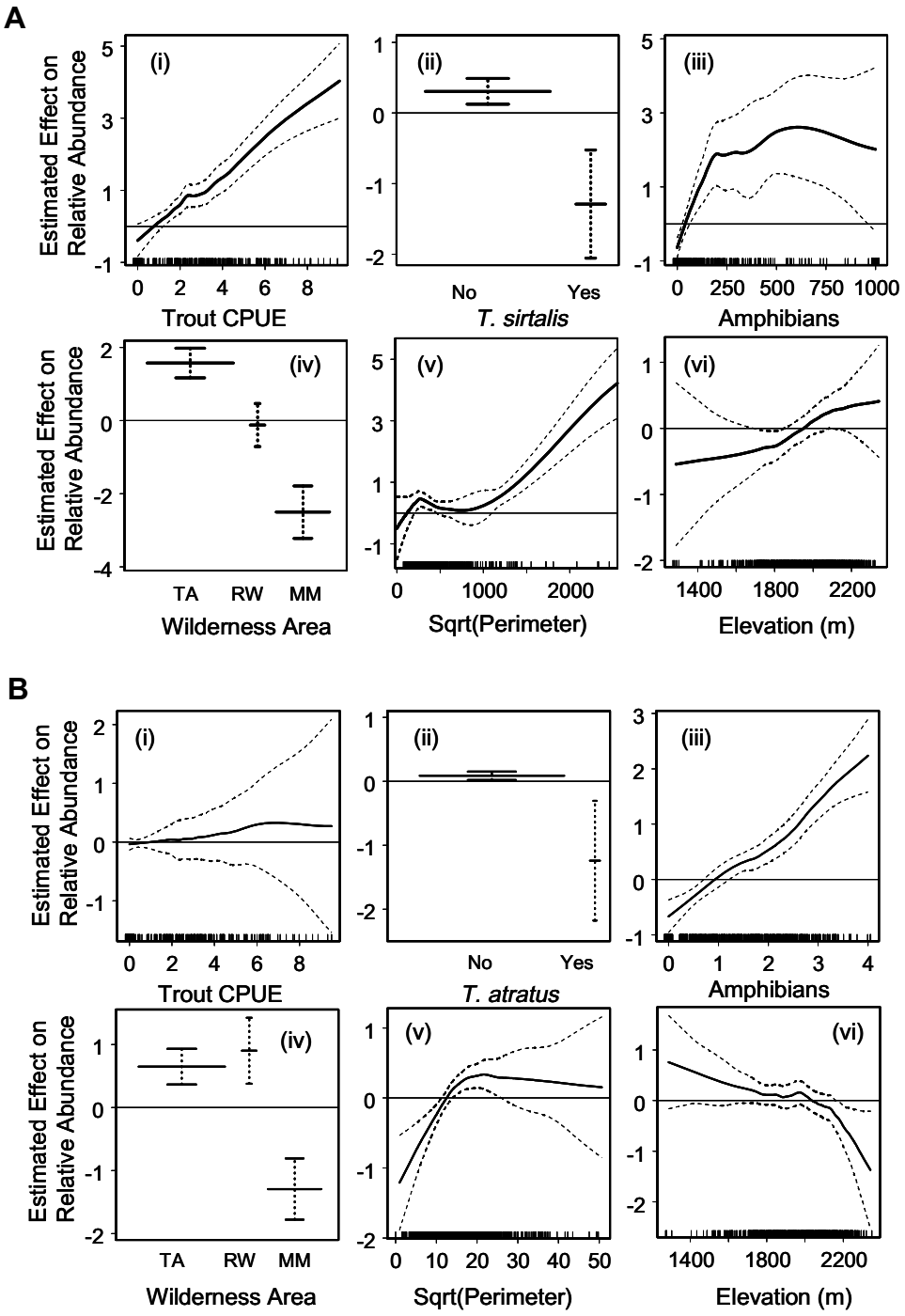

Fig. 4 – Estimated effect of each of the predictor variables used in the generalized additive model assessing the relative abundance of (A) *T. atratus* and (B) *T. sirtalis* at a water body. Response curves are based on partial residuals and are standardized to have an average probability of zero (marked by average effect line). Dashed lines on either side of the response curve represent approximate 95% confidence intervals and hatch marks at the bottom represent data points. Significance is indicated when estimated 95% bounds fall completely above or below the average effect line. Variables include (i) catch per unit effort (CPUE) of trout (ii) occurrence of the other garter snake species, (iii) relative number of amphibians observed, (iv) wilderness area (TA = Trinity Alps, RW = Russian Wilderness, MM = Marble Mountains), (v) water body perimeter, and (vi) elevation.

T. atratus. We expect that hyperpredation is occurring in this situation where a non-indigenous prey (trout) indirectly negatively affects native prey (*R. cascadae*) via facilitation of a shared predator (*T. atratus*).

This case differs from other interactions described as hyperpredation in the literature because the two prey species also interact directly via intraguild predation. Trout and amphibians can be thought of as competitors since

both primarily prey on invertebrates (Finlay and Vredenburg, 2007) in and around aquatic habitats, but trout also are predators on amphibians. When Courchamp et al. (2000) modeled hyperpredation using island birds as the indigenous prey, rabbits as the introduced prey, and feral cats as the facilitated predator; they assumed no direct interaction between the two prey species. Other well-described examples of hyperpredation also included two prey sources with minimal direct interactions (e.g., conilurine rodents and rabbits (Smith and Quin, 1996), feral pigs and island foxes (Roemer et al., 2002), and human food resources and desert tortoises (Kristan and Boarman, 2003). The additional direct predator/prey relationship between regularly stocked trout and amphibians complicates our ability to definitively demonstrate an indirect relationship between trout and *R. cascadae*. Welsh et al. (2006) found that *R. cascadae* were approximately 3.7 times more likely to be found in water bodies without trout than with trout and that amphibian abundances were significantly reduced in the presence of trout. However, our findings implicate the hyperpredation process in causing more extreme increases in predation pressures than the direct effects of trout alone or trout and *T. sirtalis*, resulting in additional decreases in native prey populations. By looking at only basins containing trout within the range of *R. cascadae*, we found an additional negative correlation with *T. atratus* presence and relative abundances of *R. cascadae*. The greater density of *T. atratus* than *T. sirtalis* in the basins where each were found also suggests that *T. atratus* could have impacts beyond that of the native predator. In addition, *T. sirtalis* was relatively common in the basins with trout and without *T. atratus* so the comparison was not between two predators versus one.

Although we did not provide direct evidence that *T. atratus* moved into these historically fishless habitats following the introduction of trout, our findings suggest this may be the case. Both the distribution and density of *T. atratus* more strongly correlated with trout compared to any other predictors assessed. At one lake in the basin study, we found *T. atratus* in 2003 prior to trout removal but never again in the three years post trout removal. We found *T. atratus* at only 7% of the water bodies surveyed in the landscape survey and the snakes were not detected in several watersheds altogether, regardless of trout densities. We likely did not identify all sites with *T. atratus* using a single-visit visual encounter technique (our estimated capture rates were only 13% in the basin study). However, in four years of repeated surveys in 16 Trinity Alps basins, we only found *T. atratus* in three basins (18%), and commonly at only two of them. The spotty distribution of *T. atratus* in the high elevations of the Klamath Mountains may reflect its relatively recent arrival following widespread trout introductions. If *T. atratus* are expanding due to introduced trout, we would expect to see invasion of *T. atratus* populations into additional basins where trout have been introduced. Alternatively, *T. atratus* may be relatively rare because they do not survive well in the high elevation, primarily lentic habitats we surveyed. Our evidence suggests this is not the case: where they were found, they were in higher densities compared to *T. sirtalis* and an equivalent proportion of both snake species had food in their stomachs. If *T. atratus* were struggling to survive in these habitats, we would have expected the opposite.

T. sirtalis was relatively common and widespread despite any negative impacts to its amphibian prey due to introduced trout. In the high elevations of the Sierra Nevada, Jennings et al. (1992), Matthews et al. (2001) and Knapp (2005) found that populations of the native western terrestrial garter snake, *Thamnophis elegans*, were closely tied to populations of native frogs, especially *R. muscosa* (mountain yellow-legged frog). Where introduced trout negatively impacted *R. muscosa* (Knapp and Matthews, 2000), the probability of finding *T. elegans* was lower than in areas with large amphibian populations (Matthews et al., 2001). Compared to the high Sierra Nevada, the diversity of highly aquatic amphibians in the Klamath Mountains is greater with eight total species and five that are commonly encountered (Welsh et al., 2006). Two of the common species are inedible to trout and can be found in large numbers with trout (Welsh et al., 2006). We found that *T. sirtalis* readily eats all of the available amphibian species including the extremely toxic *T. granulosa* (Brodie and Brodie, 1999). The higher occurrence and density of amphibian prey mediated by the higher diversity in the Klamath Mountains compared to the Sierra Nevada is likely why we did not see a similar pattern of decline as in the Sierra Nevada with *T. elegans*.

While we frequently encountered *T. sirtalis* in lentic waters during our surveys, we rarely found the species in water bodies where we found *T. atratus*. The lack of overlap may be due to exclusion by *T. atratus*. Luiselli (2006) found that high niche overlap for two species of snakes often resulted in one of the competitors being extirpated from an area.

6. Conclusions

Given the worldwide practice of stocking fish into aquatic habitats, it is important to more fully understand the consequences of the practice on food-web structure and ecosystem functioning. Recent research has shown that the introduction of trout dramatically alters community structure in high elevation lake basins. Documented food-web consequences include increased top–down effects, simplified food-web structure, and changes in habitat coupling (reviewed by Eby et al., 2006). Our evidence of an indirect bottom–up food-web effect of trout introductions via hyperpredation suggests that there are likely more unforeseen consequences to be studied and addressed so that land managers can incorporate the range of ecosystem-level effects into conservation goals and decisions. For example, the impacts of wilderness fish stocking practices in California are currently being assessed by the California Department of Fish and Game (CDFG) due to a recent California Superior Court ruling that found the agency to be remiss by not considering impacts to sensitive species when making stocking decisions. The ruling concluded that CDFG must consider the impacts of fish stocking on native sensitive species when making future stocking decisions (California Superior Court of Sacramento County, 2007). Consideration of indirect impacts such as hyperpredation is necessary for wildlife managers to make accurate assessments about the impacts of their stocking practices.

Acknowledgements

CDFG provided funding (ESA Section 6 grants E-2-F-21 and E-2-F-27) and logistical support for the landscape survey, basin study and case study. National Fish and Wildlife Foundation grants 00-154 and 04-0075 to HHW also funded the landscape survey and case study, respectively. The basin study was also funded by the National Science Foundation (grant DEB 0415505 to SPL), UC Water Resources Center (grant W-987 to SPL), and the UC Davis Wildlife Health Center/Department of Fish and Game Resource Assessment Program. K.L.P. received additional support from UC Davis Ecology Block Grants. J.M.G. received additional support from a Declining Amphibian Populations Task Force student research grant. We thank CDFG especially B. Bolster, B. Aguilar, D. Maria and E. Pert for their support and collaboration throughout the project. Field support was provided by R. Bourque, C. Wheeler, M. Larson, D. Ashton, J. Bettaso, J. Stead, K. Baumberger, J. Handwerker, N. Rujanavech, C. Mingione, C. Grattan, R. Schell, M. Alles, E. Wier, J. Jones, and many others. B. Howard and R. Knickerbocker provided database and GIS support. We thank R. Knapp and T. Schoener for helpful comments on a previous version of this paper.

REFERENCES

Belsley, D.A., Kuh, E., Welson, E.R., 1980. Regression Diagnostics. Identifying Influential Data and Sources of Collinearity. Wiley, New York.

Beyer, H.L., 2004. Hawth's Analysis Tools for ArcGIS. <http://www.spatialecology.com/htools> (accessed November 2006).

Brodie III, E.D., Brodie Jr., E.D., 1999. Predator-prey arms races. Bioscience 49, 557–568.

Brown, W.S., Parker, W.S., 1976. A ventral scale clipping system for permanently marking snakes (Reptilia, Serpentes). Journal of Herpetology 10, 247–249.

California Superior Court of Sacramento County, 2007. Pacific Rivers Council and Center for Biological Diversity v. California Department of Fish and Game, Case No. 06 CS 01451.

Cardona, L., 2006. Trophic cascades uncoupled in a coastal marsh ecosystem. Biological Invasions 8, 835–842.

Castriota, L., Scarabello, M.P., Finoia, M.G., Sinopoli, M., Andaloro, F., 2005. Food and feeding habits of pearly razorfish, *Xyrichtys novacula* (Linnaeus, 1758) in the southern Tyrrhenian Sea: variation by sex and size. Environmental Biology of Fishes 72, 123–133.

Chaneton, E.J., Bonsall, M.B., 2000. Enemy-mediated apparent competition: empirical patterns and the evidence. Oikos 88, 380–394.

Courchamp, F., Langlais, M., Sugihara, G., 1999. Control of rabbits to protect island birds from cat predation. Biological Conservation 89, 219–225.

Courchamp, F., Langlais, M., Sugihara, G., 2000. Rabbits killing birds: modeling the hyperpredation process. Journal of Animal Ecology 69, 154–164.

Crump, M.L., Scott, N.J.J., 1994. Visual encounter surveys. In: Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.-A.C., Foster, M.S. (Eds.), Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, DC, pp. 84–91.

Eby, L.A., Roach, W.J., Crowder, L.B., Stanford, J.A., 2006. Effects of stocking-up freshwater food webs. Trends in Ecology and Evolution 21, 576–584.

Finlay, J.C., Vredenburg, V.T., 2007. Introduced trout sever trophic connections in watersheds: consequences for a declining amphibian. Ecology 88, 2187–2198.

Fitch, H.S., 1984. Thamnophis couchii. Catalogue of American Amphibians and Reptiles, 351.1–351.3.

Fitch, H.S., 1987. Collecting and life history techniques. In: Seigel, R.A., Collins, J.T., Novak, S.S. (Eds.), Snakes: Ecology and Evolutionary Biology. Macmillan Publishers, New York, pp. 143–164.

Garwood, J.M., Welsh Jr., H.H., 2005. Natural history notes: *Rana cascadae* (Cascades Frog). Predation. Herpetological Review 36, 165.

Halpern, B.S., Cottenie, K., Broitman, B.R., 2006. Strong top-down control in southern California kelp forest ecosystems. Science 312, 1230–1232.

Hankin, D.G., Reeves, G.H., 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45, 834–844.

Hastie, T.J., Tibshirani, R., 1991. Generalized Additive Models. Chapman and Hall, New York.

Hobert, J.P., Altman, N.S., Schofield, C.L., 1997. Analyses of fish species richness with a spatial covariate. Journal of the American Statistical Association 92, 846–854.

Holt, R.D., 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12, 197–229.

Hurtubia, J., 1973. Trophic diversity measurement in sympatric predatory species. Ecology 54, 85–890.

Jennings, W.B., Bradford, D.F., Johnson, D.F., 1992. Dependence of the garter snake *Thamnophis elegans* on amphibians in the Sierra Nevada of California. Journal of Herpetology 26, 503–505.

Kephart, D.G., 1982. Microgeographic variation in the diets of garter snakes. Oecologia 52, 287–291.

Knapp, R.A., 2005. Effects of nonnative fish and habitat characteristics on lentic herpetofauna in Yosemite National Park, USA. Biological Conservation 121, 265–279.

Knapp, R.A., Matthews, K.R., 2000. Non-native fish introductions and the decline of mountain yellow-legged frogs from within protected areas. Conservation Biology 14, 428–438.

Knapp, R.A., Matthews, K.R., Sarnelle, O., 2001. Resistance and resilience of alpine lake fauna to fish introductions. Ecological Monographs 71, 401–421.

Knapp, R.A., Boiano, D.M., Vredenburg, V.T., 2007. Removal of nonnative fish results in population expansion of a declining amphibian (mountain yellow-legged frog, *Rana muscosa*). Biological Conservation 135, 11–20.

Kristan III, W.B., Boarman, W.I., 2003. Spatial pattern of risk of common raven predation on desert tortoises. Ecology 84, 2432–2443.

Lind, A.J., Welsh Jr., H.H., 1994. Ontogenetic changes in foraging behaviour and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*. Animal Behaviour 48, 1261–1273.

Luiselli, L., 2006. Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. Oikos 114, 193–211.

Marzluff, J.M., Millspaugh, J.J., Hurvitz, P., 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. Ecology 85, 1411–1427.

Matthews, K.R., Knapp, R.A., Pope, K.L., 2001. Garter snake distributions in high elevation ecosystems: is there a link with declining amphibians and nonnative trout introductions? Journal of Herpetology 36, 16–22.

Millspaugh, J.J., Nielson, R.M., McDonald, L., Marzluff, J.M., Gitzen, R.A., Rittenhouse, C.D., Hubbard, M.W., Sheriff, S.L., 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management 70, 384–395.

Noonburg, E.G., Byers, J.E., 2005. More harm than good: when invader vulnerability to predators enhances impact on native species. Ecology 86, 2555–2560.

Polis, G.A., Meyers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20, 297–330.

Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28, 289–316.

Pollock, K.H., Nichols, J.D., Brownie, C., Hines, J.E., 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs 107, 1–97.

Rodriguez, L.F., 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biological Invasions 8, 927–939.

Roemer, G.W., Donlan, C.J., Courchamp, F., 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. Proceedings of the National Academy of Sciences of the United States of America 99, 791–796.

Rossman, D.A., Ford, N.B., Seigel, R.A., 1996. The Garter Snakes: Evolution and Ecology. University of Oklahoma Press, Oklahoma.

S-Plus, 2001. User's Manual, Version 6. Insightful Corporation, Washington.

Scavia, D., Fahnenstiel, G.L., Evans, M.S., Jude, D.J., Lehman, J.T., 1986. Influence of salmonid predation and weather on long-term water-quality trends in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 43, 435–443.

Schindler, D.E., Knapp, R.A., Leavitt, P.R., 2001. Alteration of nutrient cycles and algal production resulting from fish introductions into mountain lakes. Ecosystems 4, 308–321.

Schoener, T.W., Spiller, D.A., 1996. Devastation of prey diversity by experimentally introduced predators in the field. Nature 381, 691–694.

Simons, L.H., 1998. *Rana cascadae* (Cascades frog): predation. Herpetological Review 29, 232.

Sinclair, A.R.E., Pech, R.P., Dickman, C.R., Hik, D., Mahon, P., Newsome, A.E., 1998. Predicting effects of predation on conservation of endangered prey. Conservation Biology 12, 564–575.

Smith, A.P., Quin, D.G., 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. Biological Conservation 77, 243–267.

Vredenburg, V.T., 2004. Reversing introduced species effects: experimental removal of introduced fish leads to rapid recovery of a declining frog. Proceedings of the National Academy of Sciences 101, 7646–7650.

Watt, J., Siniff, D.B., Estes, J.A., 2000. Inter-decadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska. Oecologia 124, 289–298.

Welsh Jr., H.H., Pope, K.L., Boiano, D., 2006. Sub-alpine amphibian distributions related to species palatability to non-native salmonids in the Klamath Mountains of northern California. Diversity and Distributions 12, 298–309.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70, 164–168.