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Importance of Native Amphibians in the Diet and Distribution of the Aquatic Gartersnake (*Thamnophis atratus*) in the San Francisco Bay Area of California

Daniel L. Preston[1] and Pieter T. J. Johnson

Department of Ecology and Evolutionary Biology, University of Colorado, Ramaley N122, Campus Box 334, Boulder, Colorado 80309 USA

Abstract.—We investigated the role of amphibian prey in the diet and distribution of the Aquatic Gartersnake (*Thamnophis atratus*) in the San Francisco Bay Area of California, USA. During surveys for amphibians and snakes at 185 ponds, we captured 139 *T. atratus*, of which 60 contained identifiable stomach contents. Native amphibians were found in 93% of the snakes containing food. Analysis of stomach contents indicated that Pacific Chorus Frogs (*Pseudacris regilla*) were the most important amphibian prey, followed by Western Toads (*Anaxyrus* [=*Bufo*] *boreas*), California Newts (*Taricha torosa*), and California Red-legged Frogs (*Rana draytonii*). The occurrence of *T. atratus* at a pond associated positively with the presence of all native amphibian species but negatively associated with the presence of introduced American Bullfrogs (*Lithobates catesbeianus* [=*Rana catesbeiana*]). The mean species richness of native amphibians at ponds where we detected *T. atratus* was also higher than that in ponds without Gartersnakes (2.45 vs. 1.74), and the odds of finding *T. atratus* at ponds with native amphibians was 12 times greater than at ponds without native amphibians. Our results underscore both the importance of native amphibians in the diet and distribution of *T. atratus* and the potential implications of ongoing amphibian declines for animals that prey on amphibians.

Global declines in amphibian populations highlight the importance of understanding the ramifications of species extinctions on ecological communities (Stuart et al., 2004; Wake and Vredenburg, 2008). In many communities, amphibians play vital roles as predators, herbivores, and prey, and their biphasic life cycles can foster energetic links between aquatic and terrestrial habitats (Gibbons et al., 2006; Regester et al., 2006). Their diverse ecological roles suggest that amphibian declines will lead to repercussions throughout ecosystems (Beard et al., 2002; Davic and Welsh, 2004; Johnson, 2006; Whiles et al., 2006). However, detailed information on species interactions, and especially trophic relationships, is required to predict potential ecological consequences of species deletions (Pimm, 1980). This information is lacking for many vertebrate species. In fact, food web ecologists have long lamented a dearth of detailed diet studies, which are needed to generate highly resolved food webs for testing ecological theory (Polis, 1991).

Natricine snakes in North America (e.g., *Thamnophis* spp.) are likely to be affected by amphibian declines because most species include amphibians in their diet (Siegel, 1996). Several reports have already suggested a possible link between amphibian losses and declines in the Mountain Gartersnake (*Thamnophis elegans elegans*) in the Sierra Nevada Mountains of California, USA, where Gartersnake distribution correlates closely with the distribution of amphibian prey (Jennings et al., 1992; Matthews et al., 2002). We suspected that the Aquatic Gartersnake (*Thamnophis atratus*) may be similarly dependent on native amphibian prey at low-elevation sites surrounding the San Francisco Bay Area in California; yet, there has not been a comprehensive study of the feeding ecology or distribution of this species in the region (Boundy, 1999).

Thamnophis atratus at lowland wetlands in California co-occurs with a diverse assemblage of pond-breeding amphibians, several of which are declining. California Red-legged Frogs (*Rana draytonii*) and certain populations of California Tiger Salamanders (*Ambystoma californiense*) are listed through the Endangered Species Act due to dramatic population declines (Fellers, 2005; Shaffer and Trenham, 2005). Western Toads (*Anaxyrus* [=*Bufo*] *boreas*; Frost et al., 2006) and California Newts (*Taricha torosa*) also have experienced moderate local declines (Jennings and Hayes, 1994; Fisher and Shaffer, 1996; Gamradt and Kats, 1996). Habitat loss and introduced species, such as Mosquitofish (*Gambusia affinis*) and American Bullfrogs (*Lithobates catesbeianus* [=*Rana catesbeiana*]; Frost et al. 2006), have been implicated as potential causes for regional amphibian declines in central California (Fisher and Shaffer, 1996; Lawler et al. 1999).

We hypothesized that *T. atratus* at low-elevation wetlands in California depends heavily on native amphibians as a food resource and that distribution patterns of this species would be positively associated with the presence and diversity of native amphibians. In contrast, we predicted that nonnative Bullfrogs and fish would associate neutrally or negatively with Gartersnakes, due to possible reductions in native amphibian prey or direct predation on snakes (Kupferberg, 1997; Crayon, 1998; Goodsell and Kats, 1999). To address these hypotheses, we surveyed 185 ponds in the San Francisco Bay Area to determine the distribution patterns of snakes relative to native amphibians, fish, and Bullfrogs, and we characterized the local diet of *T. atratus* by using stomach contents analyses. Our results provide detailed information on the ecology of a vertebrate predator and provide further evidence for the prominent roles of pond-breeding amphibians in wetland food webs.

Materials and Methods

Study Species.—Three subspecies of the Aquatic Gartersnake are recognized: *T. a. hydrophilus* from southwestern Oregon, USA, to just north of San Francisco Bay; *T. a. atratus* in the southern San Francisco Peninsula and Santa Cruz Mountains; and *T. a. zaxanthus* east of San Francisco Bay and along the coast south of the San Francisco peninsula to Santa Barbara County (Boundy, 1999). Within our study region, *T. a. zaxanthus*, *T. a. atratus*, and hybrids between the two subspecies occur, making distinguishing subspecific status in the field challenging (Boundy, 1999). Thus, we refer to all Aquatic Gartersnakes in this study as *T. atratus*, although our study specimens probably include both southern subspecies and their hybrids.

Study Region.—Between May and August 2009, we surveyed 185 ponds across four counties in the Bay Area of California for Gartersnakes and amphibians (Contra Costa, Alameda, Santa Clara, and San Mateo counties; Fig. 1). All ponds were visited

[1]Corresponding Author. E-mail: daniel.preston@colorado.edu
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once between May and July, and then a subset (n = 84) were visited a second time during July and August. We identified ponds by using a combination of USGS Landsat data, aerial photographs, and communication with local land managers. The ecoregion in this area consists of oak woodland and chaparral, whereas land uses surrounding surveyed ponds included rangeland, recreational areas, and natural preserves. Of the 185 ponds surveyed, 181 were created artificially, primarily as watering sites for livestock. Ponds included in the survey ranged from completely grazed to ungrazed, and they supported varying levels of emergent vegetation (*Typha*, *Juncus*, and *Scirpus* spp.). Surveyed ponds ranged in surface area from 59 to 8,039 m^2 and in elevation from 61 to 1,057 m.

Snake and Amphibian Surveys.—We conducted visual encounter surveys by slowly walking a pond perimeter (Vonesh et al., 2010). We captured each Gartersnake by hand and recorded the snout–vent length (SVL), sex, and the reproductive status of females (gravid or nongravid). We gently palpated each captured snake by hand to induce regurgitation of stomach contents (Fitch, 1987). In the lab, we identified, counted, and weighed (wet mass) all stomach contents on the same day they were collected. For amphibian prey items we recorded the developmental stage (larvae, metamorph, or adult) of each identifiable species.

To detect fish and amphibians at surveyed ponds, we used a combination of standardized net sweeps around pond margins and seines in deeper pond regions (modified from Heyer et al., 1994). We conducted net sweeps perpendicular to shore every 3–5 m around the margin of a pond by using a D-net (1.4-mm mesh; 2,600-cm^2 opening). We also used a seine net (4-mm mesh, 1 m in height by 2 m in width) to conduct three or four collections of approximately 5 m in length in each pond. We identified and counted all species of captured amphibians and fish during D-net sweeps and seines before releasing them back into the pond. During surveys, we also recorded pond elevation and pond area by using a GPS unit, and we visually estimated the percentage of the shoreline of each pond that was vegetated.

Analyses.—We used chi-square tests of independence to examine differences between the proportions of male and female snakes containing food, the proportions of gravid and nongravid females containing food, and the proportions of ponds with and without snakes that also supported each amphibian species or fish. Student's t-tests were used to compare mean native amphibian richness between ponds with and without *T. atratus*. We used logistic regression, Poisson regression, and simple linear regression to test for significant relationships between snake SVL and the probability of a snake containing stomach contents (yes or no), the number of prey items contained in each snake (count data), and total prey mass (log-transformed wet mass in milligrams), respectively.

We quantified snake diet by calculating the numerical percentage, frequency of occurrence, and percent by wet mass for each prey type (Hyslop, 1980). The numerical percentage (%N) was calculated as the number of each prey type divided by the total number of individual prey items recovered. Frequency of occurrence (%O) was the percentage of snakes containing each prey type divided by the total number of snakes with stomach contents. Percent by wet mass (%W) was the cumulative mass of each prey type divided by total prey mass recovered from all individuals. The index of relative importance (IRI; Pinkas et al., 1971) was used to reduce bias associated with using any one of these measures alone. IRI was calculated as %O (%N + %W) and then was converted to a percentage (%IRI) to facilitate interpretation (Pinkas et al., 1971; Cortes, 1997).

We used logistic regression to test the hypothesis that Gartersnake presence is associated positively with native amphibian presence (following Matthews et al., 2002). We predicted a priori that the following parameters could influence snake distribution: native amphibian presence, pond elevation, pond area, proportion of the shoreline vegetated, fish presence, and Bullfrog presence. Pearson's correlations were used to evaluate whether any parameters were collinear. The relative importance of each parameter was determined using likelihood ratio tests and Akaike Information Criterion (AIC) values for reduced models, each lacking the parameter of interest (Burnham and Anderson, 2002). Larger AIC values of reduced models indicate greater relative importance of the parameter removed. Lastly, we used the odds ratio to evaluate how native amphibian presence affected the odds of detecting snakes at a pond. We used PASW Statistics 18 (IBM SPSS, 2010) for all analyses. For all tests, statistical significance was assumed at α = 0.05, and we report P values as two-tailed.

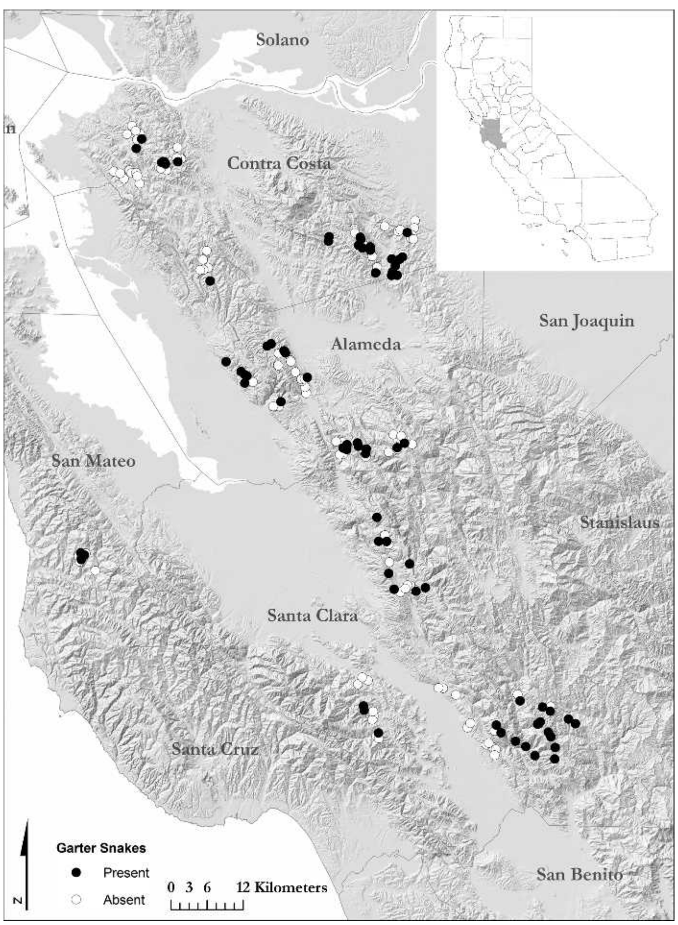

FIG. 1. Map of the study region surrounding the San Francisco Bay Area in California. The inset highlights the counties in California where surveys were conducted. Solid points indicate surveyed ponds where *Thamnophis atratus* was present, and hollow points indicate surveyed ponds where we did not detect *T. atratus*.

RESULTS

Capture Data.—We detected *T. atratus* at 78 of the 185 ponds surveyed and captured 139 individual snakes. The maximum number of snakes detected at a pond was 20 (median = 1.5, mode = 1). Of the captured snakes, 52 (37%) were male and 87

(63%) were female. Only 15 of the snakes captured (11%) were less than 15 cm in SVL, indicating very few of the individuals in the study were young of the year. We were confident in our snake detection abilities because among the wetlands that were visited twice over the summer, we only detected snakes during a second visit that were undetected on the first visit at seven of 84 sites. If snakes went undetected at some sites, we have no reason to believe that this would introduce systematic bias to our analyses.

Diet Composition.—Sixty of the 139 *T. atratus* captured (43%) contained stomach contents. Prey items included five species of pond-breeding amphibians, aquatic leeches, and slugs (Table 1). All amphibians were consumed as larvae or metamorphs, except for three adult *T. torosa*. The most commonly eaten prey included *P. regilla* (63% of snakes with stomach contents), *A. boreas* (22%), *T. torosa* (20%), and *R. draytonii* (8%). We rarely recovered *L. catesbeianus* (2%), aquatic leeches (3%), or slugs (2%). We believe the leeches and slugs represent primary prey, as opposed to secondary prey, because there were not other prey types within the same snakes that could have been predators of leeches or slugs. The %N, %O, and %W indicate that *P. regilla*, *A. boreas*, and T. *torosa* were the most significant prey types (Table 1). Among these three native amphibians, however, *P. regilla* contributed most to the diet of *T. atratus* (%IRI = 69.9; Table 1).

Patterns of Size, Sex, Gravidity and Diet.—SVL was positively correlated with total prey mass (linear regression: $r^2 = 0.18$, df = 54, $P < 0.01$) and the number of individual prey items consumed (Poisson regression: df = 58, $P < 0.001$). The largest meals by mass were held by two snakes that had each consumed one adult *T. torosa* (prey masses of 10.4 and 14.8 g), and two snakes that had each consumed 22 (total prey mass of 8.1 g) and 23 (total prey mass of 8.8 g) *A. boreas* metamorphs, respectively. Snake size (SVL) was not a significant predictor of whether an individual contained stomach contents (logistic regression: $\chi^2 = 0.30$, $P = 0.59$). Female and male snakes did not differ in their likelihood of having stomach contents ($\chi^2 = 1.58$, df = 1, $P = 0.21$) nor did gravid and nongravid females ($\chi^2 = 0.0001$, df = 1, $P = 0.99$).

Patterns of Distribution.—The presence of *T. atratus* at a pond was associated positively with native amphibian presence and species richness. Ninety-six percent of the ponds with *T. atratus* supported one or more species of native amphibians, whereas 77% of the ponds without *T. atratus* supported native amphibians ($\chi^2 = 13.01$, df = 1, $P < 0.001$; Fig. 2). Mean native species richness in ponds with *T. atratus* was 2.45 ($n = 109$, SE = 0.12), compared with 1.74 ($n = 78$, SE = 0.12) in ponds without *T. atratus* ($t = -4.06$, df = 183, $P < 0.0001$). All five species of native amphibians detected in our surveys (*P. regilla*, *A. boreas*, *T. torosa*, *R. draytonii*, and *A. californiense*) were more likely to be present in ponds with *T. atratus* than in ponds without *T. atratus*, although the difference was only significant for *P. regilla*, *R. draytonnii*, and all native species combined (Fig. 2). In contrast, nonnative Bullfrogs and nonnative fish (Bass [*Micropterus* spp.], Bluegill [*Lepomis macrochirus*], Mosquitofish, and Stickleback [*Gasterosteus aculeatus*] were grouped together for this analysis) were less common in ponds that supported *T. atratus* than in ponds without *T. atratus*; however, the difference was only statistically significant for Bullfrogs (Bullfrogs: $\chi^2 = 4.283$, df = 1, $P = 0.038$; all fish species: $\chi^2 = 2.145$, df = 1, $P = 0.143$; Fig. 2). Results of the logistic regression analysis indicate that the odds of finding *T. atratus* at a pond was 12 times higher when native amphibians were present (Table 2). Of the other parameters included in the model, Gartersnakes showed a relatively weak positive association with pond elevation and shoreline vegetation, and a negative association with Bullfrog presence (Table 2).

TABLE 1. Stomach contents of *Thamnophis atratus* from ponds in the San Francisco Bay Area of California. Columns indicate the numerical percentage of each prey type of 258 individual prey items recovered (%N), the percentage of snakes containing each prey type of 60 snakes with stomach contents (%O), the percentage of each prey type of the total wet mass of all recovered prey (%W), and percent index of relative importance (IRI = %O(%N + %W). All recovered amphibian prey were either larvae or metamorphs, except for three adult *Taricha torosa*.

Prey type	%N	%O	%W	%IRI
P. regilla	46.1	63.3	32.1	69.9
A. boreas	36.0	21.7	21.1	17.5
T. torosa	8.1	20.0	29.2	10.5
R. draytonii	3.9	8.3	10.1	1.6
L. catesbeianus	0.4	1.7	4.8	0.1
Leach	3.5	3.3	1.4	0.2
Slug	1.9	1.7	1.6	0.1

DISCUSSION

Results of our study illustrate the importance of native amphibians in the diet of Aquatic Gartersnakes within our study region. Of the individuals containing stomach contents, 56 of 60 (93%) included one or more native amphibian species (*P. regilla*, *A. boreas*, *T. torosa*, or *R. draytonii*). Gartersnake presence also was associated positively with the presence and species richness of native amphibians. Together, these results indicate that native amphibians are probably a prerequisite for the persistence of *T. atratus* within our study region.

The diet composition of Aquatic Gartersnake found at our study sites in California varies from that of several other reports (Table 3). The most comprehensive study of the feeding ecology of *T. atratus*, which involved the northern subspecies (*T. a. hydrophilus*) at a stream near the California–Oregon border, found that snakes fed primarily on Foothill Yellow-legged Frogs (*Rana boylii*), Pacific Giant Salamanders (*Dicamptodon tenebrosus*), and salmonid fish (Lind and Welsh, 1994). Another study at high-elevation lentic sites in northern California found *Pseudacris regilla*, *Anaxyrus boreas*, *Rana cascadae*, and salmonid fish in the stomach contents of *T. a. hydrophilus* (Pope et al., 2008). To our knowledge, our study is the first to report aquatic leeches and slugs in the diet of *T. atratus* and is also the first substantiated report involving consumption of *R. draytonii* and *T. torosa*. Our results, coupled with previous studies, suggest that *T. atratus* consumes primarily amphibians and fish. Differences in diet between geographic regions, and perhaps between northern and southern subspecies, probably reflect differences in prey availability, and not necessarily differences in prey preference (Fitch, 1940; Kephart, 1982). These collective findings demonstrate the importance of sampling the diet of a given species over a wide geographic area before making generalizations about feeding habits.

In contrast to previous reports of *T. atratus* diet, fish were notably absent from snake stomach contents in our study (Table 3). The small ponds surveyed in our study supported a variety of nonnative fishes, including Bass, Bluegill, Mosquitofish, and Stickleback. These species were never found in *T. atratus* stomach contents, and at the majority of the ponds with nonnative fish (23/33), we did not detect Gartersnakes. In contrast, nonnative trout (*Salvelinus fontinalis* and *Oncorhynchus mykiss*) are a significant component of the diet of *T. atratus* in the Klamath Mountains of northern California, and in this region *T. atratus* is more closely associated with lakes containing introduced fish than those with native amphibians (Pope et

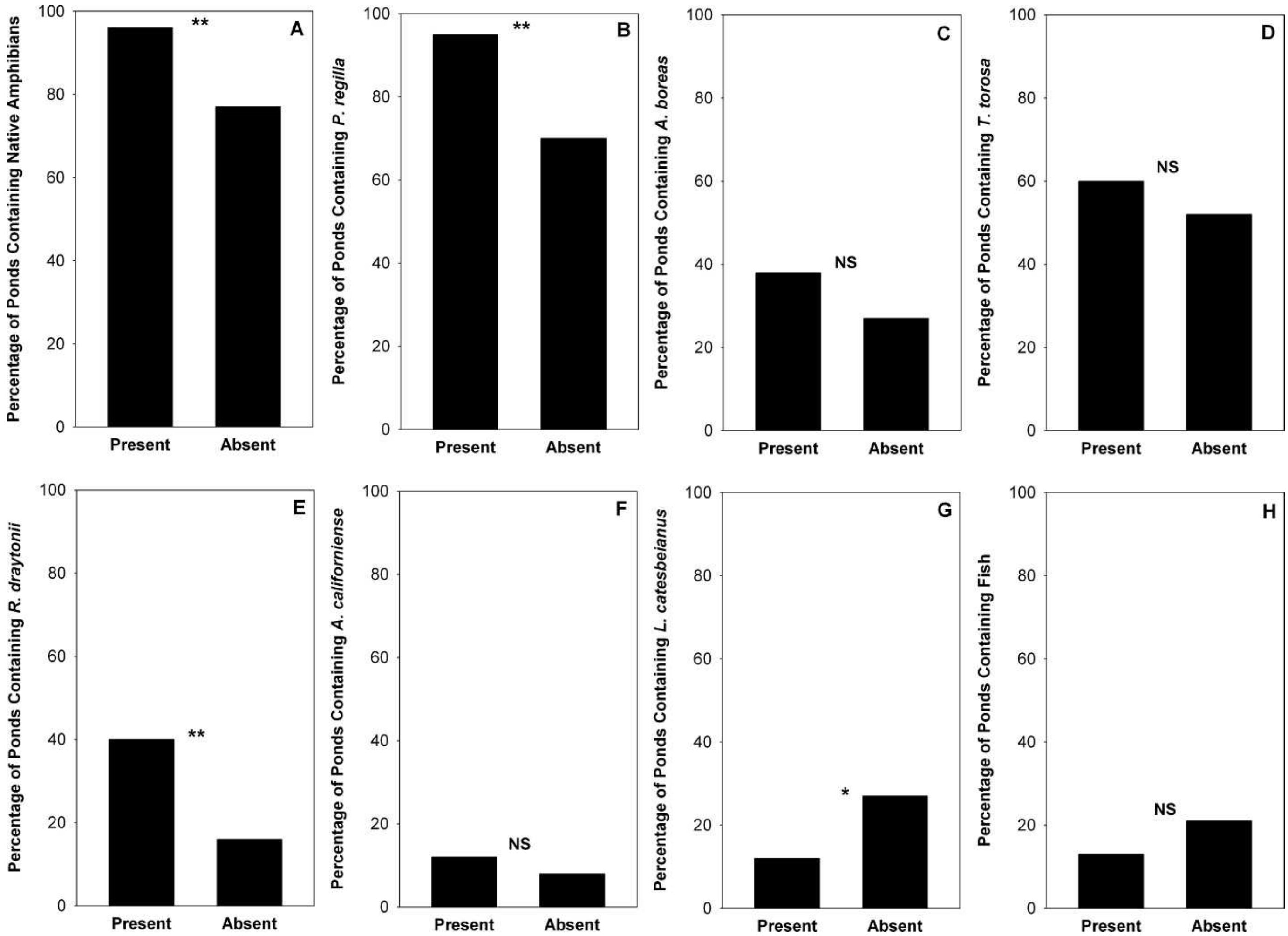

FIG. 2. Percentages of surveyed ponds where *Thamnophis atratus* was present (78 ponds) or absent (107 ponds) that also contained native amphibians (A), *Pseudacris regilla* (B), *Anaxyrus boreas* (C), *Taricha torosa* (D), *Rana draytonii* (E), *Ambystoma californiense* (F), *Lithobates catesbeianus* (G), and fish (H). Fish species included Bass (*Micropterus* spp.), Bluegill (*Lepomis macrochirus*), Mosquitofish (*Gambusia affinis*), and/or Stickleback (*Gasterosteus aculeatus*). Stars between the bars represent statistically significant differences between the percentage of ponds with and without snakes (single stars indicate $P < 0.05$, double stars indicate $P < 0.001$). NS indicates no significant difference.

al., 2008). *T. atratus* may feed readily on introduced trout because they are adapted to feeding on native salmonid prey. The nonnative pond fish in our study region may represent a more foreign food resource and are not closely related to any species that share an evolutionary history with *T. atratus*. This may partially explain why we did not detect fish in the stomach contents of snakes in our study. Although we did not find a significant effect of fish presence on the probability of detecting *T. atratus*, the invasive fish found in California ponds may reduce or eliminate populations of native amphibians, which are the primary prey of *T. atratus* (Gamradt and Kats, 1996; Goodsell and Kats, 1999; Smith et al., 2001). A similar scenario has probably occurred in the high Sierra Nevada in northern California, where introduced trout have reduced populations of amphibians and *T. e. elegans* that prey on them (Matthews et al., 2002; Vredenburg, 2004). The contrasting effects of introduced fish on the diet and range of *Thamnophis* species in different habitats highlight the importance of understanding the complex ecological consequences of fish introductions.

Although nonnative America Bullfrogs have been reported as prey for *T. atratus* in northern California (Kupferberg, 1994), the continued invasion of this species is unlikely to benefit *T. atratus* populations. A single Bullfrog metamorph was recovered from one *T. atratus* in our study. Kupferberg (1994) observed *T. a. hyrophilus* preying on larval Bullfrogs in a stream and under experimental conditions, but the handling times for consuming second-year larvae were several hours and only the largest snakes in the population were capable of feeding on Bullfrogs. These findings suggest that *T. atratus* are not likely to be effective Bullfrog predators in nature. Adult Bullfrogs are too large for consumption by *T. atratus*; in fact, *T. atratus* have actually been consumed by Bullfrogs (Crayon, 1998). Bullfrogs are likely to negatively impact *T. atratus* populations, because competitive and predatory interactions between Bullfrogs and smaller native amphibians probably reduce prey availability for *T. atratus* (Kupferberg, 1997; Kiesecker et al., 2001). This hypothesis is consistent with the results of our regression analysis that indicate that snake presence is negatively associated with bullfrog presence. Bullfrogs were detected at 38 ponds in our survey, although snakes were found at only nine of those ponds. This contrasts with the positive association observed between all native amphibians and Gartersnake presence (Fig. 2).

Our study is noteworthy in documenting the consumption of toxic Newts (*Taricha* spp.) by *T. atratus*. *Taricha* adults contain tetrodotoxin (TTX), a compound that is lethal to most vertebrate

TABLE 2. Logistic regression analysis predicting Gartersnake presence at the pond scale. AIC values compare nested models (i.e., full models minus the variable of interest). Higher AIC values indicate greater relative importance of the variable.

Variable	Likelihood ratio test statistic	AIC	*P*	Odds ratio	95% CI of odds ratio	Direction of effect
Native amphibian presence (yes vs. no)	13.3	220.9	<0.001	12.1	2.323–62.718	+
Pond elevation (m)	11.1	218.8	0.001	1.0	1.001–1.004	+
Shoreline vegetation (proportion)[a]	6.8	214.5	0.009	2.3	1.209–4.204	+
Bullfrog presence (yes vs. no)	4.1	211.8	0.042	0.4	0.148–0.999	–
Pond area (m^2)	2.0	209.6	0.156	1.0	0.999–1.000	NA[b]
Fish presence (yes vs. no)	0.0	207.6	0.969	1.0	0.327–2.923	NA

[a] Arcsine square root transformed.
[b] NA, not applicable.

predators (Mosher et al., 1964; Brodie, 1968). Although the resistance of some *T. sirtalis* populations to TTX has been known for many years (Brodie, 1968), only recently have reports documented populations of *T. couchii* and *T. atratus* feeding on adult *Taricha* (Brodie et al., 2005; Greene and Feldman, 2009). We found three *T. atratus* with adult *Taricha* in their stomachs. Two individuals were found in Alameda County and the third in Santa Clara County. Studies on the coevolution of *Thamnophis* and their toxic prey have revealed that resistance to TTX varies among *T. sirtalis* populations, probably as a response to differences in the strength of selection induced by Newt prey (Brodie et al., 2002). A similar degree of spatial variation in TTX resistance across *T. atratus* populations is probable. To date, all reports of adult *Taricha* predation by *T. atratus* have been from populations surrounding the San Francisco Bay Area in California (Greene and Feldman, 2009; Feldman et al., 2009). Not surprisingly, the San Francisco Bay Area is also a "hot-spot" of TTX resistance in *T. sirtalis* (Brodie et al., 2002). It is unclear whether *T. atratus* in other regions of its range are also resistant to TTX, and further research is needed to determine whether the geographic patterns of TTX resistance in *T. atratus* mirror those of *T. sirtalis*.

Our results have potential implications for understanding the food web consequences of ongoing amphibian population declines. The four most commonly eaten amphibian prey species in our study region vary widely in terms of current and historical population trends, complicating efforts to predict how amphibian declines will influence *T. atratus* and other amphibian predators. Some evidence exists for population declines of *A. boreas* and *T. torosa* (Jennings and Hayes, 1994; Fisher and Shaffer, 1996), whereas *R. draytonii* populations have declined significantly throughout most of their range (Fellers, 2005). Yet, populations of *P. regilla*, the most important prey species to *T. atratus* in our study region, are considered robust where appropriate habitat exists in California (Rorabaugh and Lannoo, 2005). *Pseudacris regilla* should provide a stable food resource for *T. atratus*, although the spread of nonnative species, such as Mosquitofish, may pose a future threat to *P. regilla* as well (Goodsell and Kats, 1999). Furthermore, the small wetlands in our study region do not contain abundant alternative prey species, such as salmonid fish, that could support *T. atratus* in the absence of amphibians (Pope et al., 2008). Future threats to native pond-breeding amphibians, such as increased invasions by fish and Bullfrogs, combined with the relative lack of alternative prey, suggest that the availability of suitable habitat

TABLE 3. Prey records for *Thamnophis atratus*. Northern localities are north of the San Francisco Bay Area and represent records for *T. a. hydrophilus*. Southern localities are reports from the Bay Area or more southern localities and represent *T. a. atratus*, *T. a. zaxanthus*, and hybrids between the two subspecies.

Prey	Locality	Reference
Fish		
Oncorhynchus mykiss	Northern	Lind and Welsh, 1994; Pope et al., 2008
Salvelinus fontinalis	Northern	Pope et al., 2008
Lavinia symmetricus	Northern	Fellers et al., 2006
Cottus sp. eggs	Northern	Bettaso et al., 2007
Anura		
Lithobates catesbeianus	Both	Kupferberg, 1994; this study
Rana cascadae	Northern	Garwood and Welsh, 2005
Rana boylii	Northern	Lind and Welsh, 1994
Rana draytonii	Southern	This study
Pseudacris regilla	Both	Pope et al., 2008; this study
Anaxyrus boreas	Both	Pope et al., 2008; this study
Caudata		
Dicamptodon tenebrosus	Northern	Lind and Welsh, 1994
Taricha granulosa	Southern	Greene and Feldman, 2009
Taricha torosa	Southern	Fox, 1951; this study
Aneides lugubris	Southern	Boundy, 1999
Batrachoseps attenuatus	Southern	Boundy, 1999
Ensatina eschscholtzii	Southern	Boundy, 1999
Other taxa		
Leech	Southern	This study
Slug	Southern	This study

for *T. atratus* may decrease as a result of the loss of amphibian prey resources. Sublethal effects of reduced prey availability on snakes, including reductions in reproductive output and growth, also may occur as prey resources decline (Shine and Madsen, 1997). However, we note that it would be naive to consider the effects of amphibian declines alone on Gartersnakes without also considering other synergistic threats. Habitat loss and land use changes may be the greatest current threat to both *T. atratus* and its amphibian prey at lowland sites in California (Dahl, 2000; Brinson and Malvarez, 2002).

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Literature Cited

Beard, K. H. 2002. Top-down effects of a terrestrial frog on forest nutrient dynamics. Oecologia 133:583–593.

Betasso, J. B., R. S. Studebaker, and J. M. Garwood. 2007. *Thamnophis atratus hydrophilus* (Oregon Gartersnake). Diet. Herpetological Review 38:211–212.

Boundy, J. 1999. Systematics of the Garter Snake *Thamnophis atratus* at the southern end of its range. Proceedings of the California Academy of Sciences 51:311–336.

Brinson, M. M., and A. I. Malvarez. 2002. Temperate freshwater wetlands: types, status and threats. Environmental Conservation 29:115–133.

Brodie, E. D., Jr. 1968. Investigations on the skin toxin of the adult Rough-skinned Newt, *Taricha granulosa*. Copeia 1968:307–313.

Brodie, E. D., Jr., B. J. Ridenhour, and E. D. Brodie III. 2002. The evolutionary response of predators to dangerous prey: hotspots and coldspots in the geographic mosaic of coevolution between Garter Snakes and newts. Evolution 56:2067–2082.

Brodie, E. D., III., C. R. Feldman, C. T. Hanifin, J. E. Motychak, D. G. Mulcahy, B. L. Williams, and E. D. Brodie Jr. 2005. Parallel arms races between Garter Snakes and newts involving tetrodotoxin as the phenotypic interface of coevolution. Journal of Chemical Ecology 31: 343–356.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference. 2nd ed. Springer, New York.

Cortes, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Sciences 54:726–738.

Crayon, J. J. 1998. *Rana catesbeiana* (Bullfrog). Diet. Herepetological Review 29:232.

Dahl, T. E. 2000. Status and trends of wetlands in the conterminous United States: 1986 to 1997. U.S. Department of the Interior, Fish and Wildlife Service. Washington, DC.

Davic, R. D., and H. H. Welsh Jr. 2004. On the ecological roles of salamanders. Annual Review of Ecology, Evolution, and Systematics 35:405–434.

Feldman, C. R., E. D. Brodie Jr., E. D. Brodie III, and M. E. Pfrender. 2009. The evolutionary origins of beneficial alleles during the repeated adaptation of Garter Snakes to deadly prey. Proceedings of the National Academy of Sciences USA 106:13415–13420.

Fellers, G. 2005. *Rana draytonii* Baird and Girard, 1852(b). California Red-legged Frog. *In* M. Lanoo (ed.), Amphibian Declines: The Conservation Status of United States Species, pp. 552–554. University of California Press, Berkeley, CA.

Fellers, G. M., J. Dhundale, and K. Ruiz. 2006. *Thamnophis atratus* (Aquatic Gartersnake). Predation. Herpetological Review 37:235–236.

Fisher, R. N., and H. B. Shaffer. 1996. The decline of amphibians in California's Great Central Valley. Conservation Biology 10:1387–1397.

Fitch, H. S. 1940. A biogeographical study of the ordinoides artenkreis of Garter Snakes (genus *Thamnophis*). University of California Publications in Zoology 44:1–150.

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

Fox, W. 1951. Relationships among the Garter Snakes of the *Thamnophis elegans* rassenkreis. University of California Publications in Zoology 50:485–530.

Frost, D. R., T. Grant, J. Faivovich, R. H. Bain, A. Haas, C. F. B. Haddad, R. O. De Sa, A. Channing, M. Wilkinson, S. C. Donnellan, et al. 2006. The amphibian tree of life. Bulletin of the American Museum of Natural History 297:1–370.

Gamradt, S. C., and L. B. Kats. 1996. Effect of introduced Crayfish and Mosquitofish on California Newts. Conservation Biology 10:1155–1162.

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

Gibbons, J. W., C. T. Winne, D. E. Scott, J. D. Wilson, X. Glaudas, K. M. Andrews, B. D. Todd, L. A. Fedewa, L. Wilkinson, R. N. Tsaliagos et al. 2006. Remarkable amphibian biomass and abundance in an isolated wetland: implications for wetland conservation. Conservation Biology 20:1457–1465.

Goodsell, J. A., and L. B. Kats. 1999. Effect of introduced Mosquitofish on pacific treefrogs and the role of alternative prey. Conservation Biology 13:921–924.

Greene, R. R., and C. R. Feldman. 2009. *Thamnophis atratus atratus*. Diet. Herpetological Review 40:103–104.

Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. A. C. Hayek, and M. S. Foster. 1994. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, DC.

Hyslop, E. J. 1980. Stomach contents analysis: a review of methods and their application. Journal of Fish Biology 17:411–429.

IBM SPSS. 2010. PASW Statistics 18 Core System User's Guide. IBM SPSS, Chicago, IL.

Jennings, M. R., and M. P. Hayes. 1994. Amphibian and reptile species of special concern in California. California Department of Fish and Game, Inland Fisheries Division, Final Report. Rancho Cordova, CA.

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

Johnson, P. T. J. 2006. Amphibian diversity: decimation by disease. Proceedings of the National Academy of Sciences USA 103:3011–3012.

Kephart, D. G. 1982. Microgeographic variation in the diets of Garter Snakes. Oecologia 52:287–291.

Kiesecker, J. M., A. R. Blaustein, and C. L. Miller. 2001. Potential mechanisms underlying the displacement of native Red-legged Frogs by introduced bullfrogs. Ecology 82:1964–1970.

Kupferberg, S. J. 1994. Exotic larval bullfrogs (*Rana catesbeiana*) as prey for native Garter Snakes: functional and conservation implications. Herpetological Review 25:95–97.

Kupferberg, S. J. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. Ecology 78:1736–1751.

Lawler, S. C., D. Dritz, T. Strange and M. Holyoak. 1999. Effects of introduced mosquitofish and bullfrogs on the threatened California Red-legged Frog. Conservation Biology 13:613–622.

Lind, A. J., and H. H. Welsh Jr. 1994. Ontogenetic changes in foraging behavior and habitat use by the Oregon Garter Snake, *Thamnophis atratus hydrophilus*. Animal Behavior 48:1261–1273.

Matthews, K. R., R. A. Knapp, and K. L. Pope. 2002. Garter Snake distributions in high-elevation aquatic ecosystems: is there a link with declining amphibian populations and nonnative trout introductions? Journal of Herpetology 36:16–22.

Mosher, H. S., F. A. Fuhrman, H. D. Buchwald, and H. G. Fisher. 1964. Tarichatoxin-tetrodotoxin: a potent neurotoxin. Science 144:1100–1110.

PIMM, S. L. 1980. Food web design and the effects of species deletion. Oikos 35:139–149.

PINKAS, L. M., S. OLIPHANT, AND I. L. K. IVERSON. 1971. Food habits of Albacore, Bluefin Tuna, and Bonito in California waters. California Department of Fish and Game Fish Bulletin 152:1–105.

POLIS, G. A. 1991. Complex trophic interactions in desserts: an empirical critique of food-web theory. American Naturalist 138:123–155.

POPE, K. L., J. M. GARWOOD, H. H. WELSH JR., AND S. P. LAWLER. 2008. Evidence of indirect impacts of introduced trout on native amphibians via facilitation of a shared predator. Biological Conservation 141:1321–1331.

REGESTER, K. J., K. R. LIPS, AND M. R. WHILES. 2006. Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. Oecologia 147:303–314.

RORABAUGH, J. C., AND M. J. LANNOO. 2005. *Pseudacris regilla* Baird and Girard, 1852(b). Pacific Treefrog. *In* M. Lanoo (ed.), Amphibian Declines: The Conservation Status of United States Species, pp. 478–484. University of California Press, Berkeley, CA.

SHAFFER, H. B., AND P. C. TRENHAM. 2005. *Ambystoma californiense* Gray, 1853. California Tiger Salamander. *In* M. Lanoo (ed.), Amphibian Declines: The Conservation Status of United States Species, pp. 605–608. University of California Press, Berkeley, CA.

SHINE, R., AND T. MADSEN. 1997. Prey abundance and predator reproduction: rats and pythons on a tropical Australian floodplain. Ecology 78 1078–1086.

SIEGEL, R. A. 1996. Ecology and conservation of Garter Snakes. *In* D. A. Rossman, N. B. Ford, and R. A. Seigel. The Garter Snakes: Evolution and Ecology, pp. 55–89. University of Oklahoma Press, Norman, OK.

SMITH, G. R., J. E. RETTIG, G. G. MITTELBACH, J. L. VALIULIS, AND S. R. SCHAACK. 2001. The effects of fish on assemblages of amphibians in ponds: a field experiment. Freshwater Biology 41:829–837.

STUART, S. N., J. S. CHANSON, N. A. COX, B. E. YOUNG, A. S. L. RODRIGUES, D. L. FISCHMAN, AND R. W. WALLER. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.

VONESH, J. R., J. C. MITCHELL, K. HOWELL, AND A. J. CRAWFORD. 2010. Rapid assessments of amphibian diversity. *In* C. K. Dodd Jr. (ed.), Amphibian Ecology and Conservation: A Handbook of Techniques, pp. 263–280. Oxford University Press, New York.

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 USA 101:7646–7650.

WAKE, D. B., AND V. T. VREDENBURG. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences USA 105:11466–11473.

WHILES, M. R., K. R. LIPS, C. M. PRINGLE, S. S. KILHAM, R. J. BIXBY, R. BRENES, S CONNELLY, J. C. COLON-GAUD, M. HUNTE-BROWN, A. D. HURYN ET AL. 2006. The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. Frontiers in Ecology and the Environment 4:27–34.

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