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Dependence of the Garter Snake *Thamnophis elegans* on Amphibians in the Sierra Nevada of California

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Thamnophis elegans (western terrestrial garter snake) is the only garter snake inhabiting the Sierra Nevada above approximately 2400 m elevation (Stebbins, 1985), ranging up to at least 3400 m elevation (pers. obs.). In this region its geographic range largely overlaps that of five species of aquatic-breeding amphibians: *Ambystoma macrodactylum* (long-toed salamander); *Bufo boreas* (western toad); *B. canorus* (Yosemite toad); *Pseudacris* [=*Hyla*] *regilla* (Pacific treefrog); and *Rana muscosa* (mountain yellow-legged frog) (Stebbins, 1985). Together, these amphibians breed in a variety of habitats, including both permanent and ephemeral waters such as lakes, ponds, shallow meadow pools, and stream pools. *Thamnophis e. elegans*, the subspecies inhabiting the Sierra Nevada, is known to depend heavily on at least some of these species as prey: *Bufo* spp. (Fitch, 1941; Cunningham, 1955; Arnold and Wassersug, 1978); *P. regilla* (Fitch, 1941; Cunningham, 1955; White and Kolb, 1974; Arnold and Wassersug, 1978); and *R. muscosa* (pers. obs.). In the present study we document the distribution of *T. elegans* in the high Sierra relative to the distribution of these amphibians, and test the hypothesis that *T. elegans* is dependent on amphibians to such an extent that the presence of amphibians at a site is a prerequisite for its existence. An implication of such a dependence would be that as local amphibian populations become extinct in the Sierra Nevada, which has been observed in recent decades (Wake, 1991; Bradford et al., unpubl. obs.), *T. elegans* may also disappear.

We surveyed for *T. elegans* as part of a study of amphibian distribution and associated water chemistry above 2440 m elevation in the Sierra Nevada. We included *T. elegans* in the study during 1991 when a randomly-selected subset of 15 of the 30 total survey areas was searched. The center of each survey area was randomly selected from a uniform grid established by the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program. Each survey area consisted of a 15 km^2 circle (i.e., 4.4 km diameter) with the selected point in the center, exclusive of any portion of the circle that was below 2440 m elevation. Two individuals (Jennings and Johnson) searched each survey area in a manner designed to provide data for sites that contain each amphibian species and sites that do not, and to ascertain whether a breeding population of each species exists in the survey area. Survey areas were searched during daytime in early and midsummer (12 June to 2 August) when amphibian larvae are present and most visible and abundant in shallow water near shore (Bradford, 1984). The survey areas were searched in a non-random manner until five "different or separate" sites containing larvae of each amphibian species were found, or until enough of the survey area had been searched to be confident that a breeding population of a species did not exist in the survey area. "Different or separate" sites were defined as ones separated by more than 200 m or ones that appeared to differ in water characteristics or sources (e.g., a pool in a stream versus an isolated pond). Sites were surveyed for amphibian larvae and *T. elegans* by

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TABLE 1. Presence/absence of amphibians at 12 sites where *Thamnophis elegans* was found. *Ambystoma macrodactylum* is omitted because it was not found in any survey area. "+" = present; "−" = absent.

Survey area	Site no.	Number of *T. elegans*	Presence/absence of amphibians: Any Species	*P. regilla*	*Bufo* spp.	*R. muscosa*
A	1	1	+	+	−	−
B	2	3	+	+	+	−
C	3	3	+	+	−	−
D	4	1	+	+	−	−
	5	1	+	+	−	−
E	6	4	+	+	−	−
	7	3	+	+	−	−
F	8	1	+	−	+	−
	9	1	+	+	−	−
G	10	1	+	+	+	−
	11	1	+	+	−	−
	12	2	+	+	−	−
Totals for *T. elegans* sites:						
7	12	22	12	11	3	0
Totals for all sites:						
15	115	22	73	59	10	15

TABLE 2. Probability (P) that all sites containing *T. elegans* also contain amphibians. P is computed as the product of the frequency of sites with amphibians within each survey area (F) for all 12 sites with *T. elegans*, i.e., $P = F_1 \cdot F_2 \cdot \ldots \cdot F_{12}$, where subscripts represent the 12 sites. F is computed as the fraction: number of sites with amphibians/total sites searched.

Survey area	Total sites	No. sites with *T. elegans*	Frequency of sites with amphibians (F)
A	16	1	0.625
B	13	1	0.615
C	11	1	0.364
D	4	2	1.000
E	7	2	0.429
F	12	2	0.500
G	9	3	0.889
Totals	72	12	

$P = 0.0045$.

walking near or in shallow water near shore. Also surveyed were up to five "different or separate" sites that appeared to represent potential breeding habitat for each amphibian species, but which lacked the species.

Individual *T. elegans* were usually captured, examined, and released. They were defined as "small" if they appeared shorter than approximately 18 cm snout-vent length, and as "large" if longer than this. "Small" individuals were presumably young of the year (White and Kolb, 1974).

Twenty-two *T. elegans* (10 small/12 large) were found in 7 of the 15 survey areas and 12 of the 115 individual sites (Table 1). Neither *T. elegans* nor amphibians were found in 3 of the 15 survey areas. *Thamnophis elegans* occurred only in sites where amphibians were present (Table 1). The probability that *T. elegans* would occur by chance only at sites where amphibians were present was extremely low ($P = 0.0045$; Table 2).

Thamnophis elegans was found primarily in association with *P. regilla* (Table 1). It occurred with *P. regilla* alone (N = 9 sites), *P. regilla* and *Bufo* spp. together (N = 2), and *Bufo* spp. alone (N = 1), but at no sites with *R. muscosa*. These differences appear to be due largely to the differences in relative abundance of the three amphibian genera, because *P. regilla* was by far the most frequently represented amphibian in the survey (Table 1). Comparisons of presence/absence of *T. elegans* versus each amphibian species showed a significant relationship only for *P. regilla* ($\chi^2 = 7.03$, df 1, $P < 0.01$ for *P. regilla*; Fisher exact test, $P > 0.10$ for *Bufo* spp. and *R. muscosa*).

The habitats in which *T. elegans* was found generally were in the lodgepole pine (*Pinus murrayana*) zone, in or adjacent to permanent ponds with emergent vegetation or shallow ephemeral meadow ponds. Elevation ranged from 2510 to 3260 m. Individuals were found swimming in ponds (18 of 22), along the shoreline of ponds (3), or within 1 m of a small creek (1). *Thamnophis elegans* was never found in or near standing or running water containing fish rather than amphibians.

This study shows that the occurrence of *T. elegans* in the Sierra Nevada at high elevation is strongly associated with the presence of amphibians. Indeed, it is possible that the presence of amphibians is a prerequisite for the existence of *T. elegans* in this region. *Thamnophis elegans* here may depend on amphibians as its primary food source. *Thamnophis e. elegans* elsewhere preys primarily on amphibians, especially recently metamorphosed *P. regilla* and *B. boreas*, although it often takes a variety of other prey including fish, leeches, mammals, lizards, and slugs (Fitch, 1941; Cunningham, 1955; White and Kolb, 1974; Arnold and Wassersug, 1978). Indeed, *T. e. elegans* in some areas appears to prefer amphibian prey, but switches to alternative prey such as fish and leeches in years when amphibians are not available (Arnold and Wassersug, 1978).

Interestingly, *T. e. elegans* in the high Sierra appears to be strictly an aquatic garter snake, whereas elsewhere in its range its inhabits primarily terrestrial habitats (Fitch, 1940; Cunningham, 1955; Stebbins, 1985). In this study we found 18 of the 22 snakes swimming in water, and no individuals more than a meter from standing water, despite travelling many kilometers through terrestrial habitats within each survey area. Indeed, the vast majority of the time spent and area traversed in the study areas was in terrestrial habitats. This apparently anomalous association with the aquatic environment has been observed in northeastern California, where *T. e. elegans* occurs in aquatic habitats in a generally arid region (Fitch, 1940). Fitch argued that *T. e. elegans* is primarily aquatic in northeastern California because humid terrestrial habitats are scarce and other species of *Thamnophis*, which are typically aquatic, are absent. Such may also be the case with *T. e. elegans* in the Sierra

Nevada at high elevation. Terrestrial habitats beyond the typically narrow riparian zone are quite arid in comparison to many terrestrial habitats at lower elevation and farther north within the range of *T. e. elegans*. Moreover, neither *T. couchi* nor *T. sirtalis* extend above approximately 2400 m elevation in the Sierra Nevada (Stebbins, 1985; pers. obs.).

In this study *T. elegans* was not found at sites containing *R. muscosa*, although this apparent lack of association was not statistically significant. It is unlikely that *T. elegans* avoids *R. muscosa* because one of us (Bradford) has observed *T. elegans* at other sites containing only *R. muscosa*, and has verified consumption of both adults and tadpoles of this species by inducing regurgitation of snakes. Moreover, *Thamnophis* are often major predators of other ranid frogs (e.g., Licht, 1974).

During the past several decades, *B. canorus* and *R. muscosa* have disappeared from many localities at high elevation in the Sierra Nevada (Phillips, 1990; Bradford et al., 1992; D. L. Martin, pers. comm.; Sherman and Morton, pers. comm.). Estimates of the magnitude of these apparent extinctions are about 50% or more of populations extant in 1950 for both species (Bradford et al., unpubl. obs.; D. L. Martin, unpubl. obs.). In contrast, *P. regilla* continues to remain an abundant and widespread amphibian in the high Sierra, and it shows no evidence of recent population declines (Bradford et al., unpubl. obs.). Reasons for the declines of *B. canorus* and *R. muscosa* are not clear (Bradford et al., 1992), but may be related to the recent population declines of many amphibians around the world (Wake, 1991). An implication from the present study is that *T. elegans* should not be dramatically affected by declines of *B. canorus* and *R. muscosa*, because *T. elegans* appears to be more strongly associated with *P. regilla* than these species, and *P. regilla* is far more widespread (Table 1). However, if populations of *P. regilla* become extinct like many populations of *B. canorus* and *R. muscosa*, sympatric populations of *T. elegans* may also suffer the same fate.

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Northernmost Record of *Desmognathus ochrophaeus*: Biochemical Identification in the Chateauguay River Drainage Basin, Québec

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The two most common species of the salamander genus *Desmognathus*, *D. fuscus* and *D. ochrophaeus*, are widespread in Eastern North America (Conant and Collins, 1991). Their similar external morphologies, overlapping ranges, high degrees of intraspecific variation, and propensity for hybridization have presented difficulties for field identification in regions of sympatry (Karlin and Guttman, 1986; Conant and Collins, 1991). Isozyme electrophoresis has therefore become a useful tool for the identification of individuals, especially within hybrid zones (Tilley et al., 1978; Karlin and Guttman, 1981; Tilley and Schwerdtfeger, 1981; Karlin et al., 1984; Karlin and Guttman, 1986; Tilley, 1988). To date, *D. fuscus* is the only member of the genus documented in the Chateauguay River drainage basin in southern Québec (Conant and Collins, 1991). In this paper we present biochemical data documenting the northernmost record of *D. ochrophaeus*, and the first record for this species in the basin.

During a survey of a brook (310 m elevation) on Covey Hill, Québec, at the northernmost edge of the Adirondack Mountains (45°01′18″N, 73°49′13″E; 340 m elevation), we discovered *Desmognathus* with variable dorsal coloration. The brook is part of the Chateauguay River drainage basin (Ministère des Terres et Forêts du Québec, 1971), which drains northward into the St. Lawrence River. The brook is spring fed