Diet and Foraging Behavior of the Terrestrial Gartersnake (Thamnophis elegans) along a Stream within the Shrub-Steppe of Central Washington State

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DIET AND FORAGING BEHAVIOR OF THE TERRESTRIAL GARTERSNAKE (*THAMNOPHIS ELEGANS*) ALONG A STREAM WITHIN THE SHRUB-STEPPE OF CENTRAL WASHINGTON STATE

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ABSTRACT—We investigated the diet and foraging behavior of a putative generalist predator, the Terrestrial Gartersnake, (*Thamnophis elegans*) along a stream in central Washington State, USA. Snakes were collected, with the sex, mass, and snout-vent length (SVL) of each recorded. Snakes were categorized by SVL into 3 groups (<300, 301–500, and >500 mm SVL). Snake SVL and mass ranged from 190–723 mm SVL ($\bar{x}$ = 425, s = 140.41), and 3.6–150.5 ($\bar{x}$ = 43.3, s = 38.5) respectively. Of the 263 snakes collected, 138 contained 141 prey items. The most abundant prey items were crayfish (n = 79, 56.2% of total), followed by cottid (n = 32, 22.6%) and cyprinid (n = 17, 12.0%) fish, and slugs (n = 13, 9.2%). The smallest group of snakes fed primarily on cyprinid fish and some slugs. These snakes foraged (sit and wait within runs), while perched on rocks or logs. The intermediate size class foraged along riffles, runs, and in pools, and had the broadest diet, feeding on cottid and cyprinid fish, crayfish, and slugs. The largest snakes were the most specialized, feeding primarily on crayfish while foraging in pools. Our data show that some individuals in this population of *T. elegans* undergo an ontogenetic shift in both diet (vertebrate to invertebrate) and foraging behavior (sit and wait to underwater foraging). This is also the 1st population of *Thamnophis* documented to feed primarily on crayfish.

Key words: diet, foraging behavior, Terrestrial Gartersnake, *Thamnophis elegans*, Washington State

Ecological studies on snakes have focused on a variety of life history traits, such as reproductive mode or output (Madsen and Shine 2000), growth and maturation (Shine 1980), thermal biology (Plummer 1997), and the evolution of diets (de Queiroz and Rodriguez-Robles 2006). Many groups of snakes are some of the most extensively studied of squamate reptiles, with the diet and feeding behavior of a variety of species well documented (Godley 1980; Kardong 1982; Kardong and Smith 2002).

Gartersnakes (*Thamnophis* spp.) are some of the best known of any temperate species of snakes (Rossman and others 1996). *Thamnophis* is a widespread genus found throughout much of North and Central America in many different habitat types, and these snakes feed on a wide range of prey items (Stebbins 2003). Some

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species of *Thamnophis* are considered dietary specialists, such as the Northwestern Gartersnake (*T. ordinoides*), or generalists like the Common Gartersnake (*T. sirtalis*) and the Terrestrial Gartersnake (*T. elegans*). Because of their broad distributions and abundance, detailed ecological studies have focused on these latter 2 species (Gregory 1984a; Peterson and others 1998; Bronikowski and Arnold 1999; Nelson and Gregory 2000).

Both diet and foraging behavior of gartersnakes may vary interspecifically (Fitch 1941; Gregory 1978), ontogenetically (Lind and Welsh 1994; de Queiroz and others 2001), temporally (Kephart and Arnold 1982), and spatially (Kephart 1982; Gregory 1984b). Species with highly specialized diets may also engage in specialized foraging behavior (Drummond 1983; Macias-Garcia and Drummond 1988, 1994). Gartersnakes also display sexual size dimorphism (Shine 1994); however, such a difference in body size may not lead to differences in foraging behavior or prey preference (Krause and Burghardt 2001).

For our study we investigated the diet and foraging behavior of a putative generalist, *T. elegans*. We sought to elucidate any ontogenetic and sex differences in diet, foraging behavior, and stream use within this population. We compare our data to previous work on *T. elegans*, and to what is known about diet and foraging in *Thamnophis*.

METHODS

Sampling Techniques and Study Area

Snakes were collected opportunistically from May through September 2005. Surveys were conducted from 08:30 to 20:30. We surveyed a 1-km stretch of Umtanum Creek (UTM: Zone 10 689446E, 5192793N, WGS84), a perennial, non-regulated stream 10 to 15 m in width, and nearly 22 km in length. Umtanum Creek drains into the Yakima River approximately 22.6 km south of Ellensburg, Kittitas County, Washington. We used visual encounter surveys (Crump and Scott 1994) to collect snakes. One observer walked along each side of the creek, while a 3rd observer walked slowly upstream in the stream channel. We attempted to approach snakes in a manner that would not disturb their normal foraging behavior.

The vegetation along Umtanum Creek is typical of riparian zones within the shrub-steppe of central Washington (Franklin and Dyrness 1973). Black Cottonwood (*Populus trichocarpa*), Quaking Aspen (*P. tremuloides*), and Ponderosa Pine (*Pinus ponderosa*) are the most common trees. Blue Elderberry (*Sambucus cerulea*), Ocean Spray (*Holodiscus bicolor*), chokecherry (*Prunus* spp.) and currants (*Ribes* spp.) are the most common shrubs, sometimes forming a continuous thicket along the creek. The upland area adjacent to the creek comprises open talus interspersed with a mix of Bitterbrush (*Purshia tridentata*), rabbitbrush (*Chrysothalmus* spp.), and Big Sage (*Artemesia tridentata*).

Specimen and Prey Item Data

Sex, mass, and snout-vent length (SVL) of all snakes collected were recorded. Individuals were placed into 3 size classes (<300 mm, 301–500 mm, and >500 mm) using life-history data (reproductive age and growth rates) available for this population of *T. elegans* (Weaver, unpubl. data). The position of each snake relative to the creek was recorded and assigned to 1 of 3 stream habitat categories: run, riffle or pool (Hawkins and others 1998). Snakes were classified using 1 of 3 foraging behaviors: sit and wait within the creek (middle of creek, perched on a rock or log), forage from shore, or forage underwater (modified from Drummond 1983). Prey items were classified as 4 types: slugs, cyprinid fish, cottid fish, or crayfish. Orientation of prey items was also recorded as either head-first, tail-first, or bent-double. Prey items were collected by inverting a snake and gently palpating the stomach (Fitch 2001). Regurgitated whole prey items were weighed to the nearest 0.1 g. Most prey items were offered back to snakes, those not re-ingested were fixed in 10% buffered formalin, and stored in 70% ethanol. Each snake was marked by clipping a unique combination of ventral and subcaudal scales (Fitch 2001). We quantified habitat types (riffle, runs, and pools) as a proportion (measured in meters) of each relative to the 1-km stretch of the creek surveyed. Prey availability was quantified as the relative abundance of prey/1 m^2 of the creek. We searched for crayfish and cottids by turning rocks along 2 randomly selected 100 m stretches of the creek.

Statistical Analysis

We used multivariate and univariate statistical analysis methods. Multivariate methods allowed us to take a holistic approach to looking at a suite of feeding behaviors simultaneously. The univariate approach allowed us to look at more detailed responses. For our multivariate approach, we used distance-based redundancy analysis (db-RDA) together with a model selection procedure to determine which combination of variables best accounted for variability in feeding behaviors (Legendre and Anderson 1999; Burnham and Anderson 2002). Distance-based redundancy analysis uses ordinary redundancy analysis on scores generated from a principle coordinate analysis (PCoA) using any distance measure of choice. The method is analogous to multivariate ANOVA except that it relies on permutations to test hypotheses. We used a suite of size and sex explanatory variables against a response matrix of snakes ordinated by 15 different foraging behaviors. Our hypothesis was that size, sex, or both would explain foraging behavior of snakes. All hypothesis tests used 9999 permutations. Following model comparison methods we display the first 2 dimensions of the PCoA solution that was used for db-RDA. The PCoA used the variance-adjusted correlation method of Legendre and Gallagher (2001) to show positions of individual foraging behaviors in the ordination space. We used univariate chi-square contingency tables (R × C test of independence) to analyze frequency of stream use, foraging behavior, and prey types consumed by each of the size classes of snakes. Linear regression analysis was used to compare the relationship between snake SVL and prey mass. Unpaired t-tests were used to compare mean prey size. All means are reported with standard deviations (*s*), and significance was set at $P = 0.05$.

RESULTS

A total of 263 snakes ($\bar{x} = SVL = 425$, $s = 140.41$, range 190–723 mm) were collected during 36 d of searching, with no recaptured snakes. One hundred and thirty-eight snakes (52.4%) contained 141 prey items. Of the 65 snakes <300 mm, 56.9% ($n = 37$) contained prey. Ninety-eight snakes 301–500 mm were
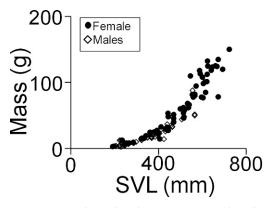

FIGURE 1. Relationship between mass and snake SVL by sex for *Thamnophis elegans* ($n = 119$) collected at Umtanum Creek, Washington, May through September 2005.

captured and 41.8% ($n = 41$) contained prey. Of the 100 captured individuals >500 mm, 60% ($n = 60$) contained prey.

Clear sexual dimorphism occurred where females had a larger SVL and mass than did males (Fig. 1). We had complete data for 166 individuals for multivariate analysis. Model selection showed the most parsimonious model to be one where animals were separated into the 3 a priori determined size classes, which was 185 times more likely to be more parsimonious than the null model (Table 1). Permutation tests showed these results to be significantly different than random permutations of foraging behavior ($F = 15.76$, $P < 0.001$). The model that included an interaction term for the sex of the animal was also significant ($F = 8.02$, $P < 0.001$) and had a 12% probability relative to the 19% of the highest ranked model. We partitioned the variance among the terms of the full model with the result that 32% of forage behavior variability could be explained by the SVL class, 3% by sex, 2% by the interaction of class and sex, leaving 63% of the foraging behavior unexplained. Snout-vent length better discriminated foraging behavior than did mass measurements. Even though there was sexual dimorphism, sex alone was not a strong model ($w_i = 0.01$).

The first 2 axes of the PCoA captured 66% of the variability in foraging behavior. The 1st axis was associated mostly with river habitat (run, riffle, or pool) and forest canopy cover (open, closed, or patchy), while the 2nd axis showed a

TABLE 1. Distance-based redundancy analysis (db-RDA) model selection based on Akaike Information Criterion with correction for small sample size (AICc), based on a Bray-Curtis distance matrix derived from a matrix of 116 individual animals (n for all models) and 15 foraging behavior characteristics. Model explanatory variables included ''SVL'', ''Sex'' (for example, male or female), ''Mass'', and ''Class'' (for example, 3 size classes: <300; 301–500; >500 mm SVL). Individuals of *Thamnophis elegans* were collected from May through September 2005 at Umtanum Creek, Kittitas County, Washington.

Model	Variable estimate	K	AICc	w_i	Evidence ratio
Class	0.259	2	−63.95	0.19	1
SVL	0.261	2	−63.56	0.16	1
Class + Sex	0.251	3	−63.42	0.15	1
Class * Sex	0.243	4	−62.91	0.12	2
SVL + Sex	0.254	3	−62.83	0.11	2
SVL * Sex	0.245	4	−62.50	0.09	2
Mass	0.267	2	−62.42	0.09	2
Mass + Sex	0.263	3	−61.07	0.05	4
Mass * Sex	0.254	4	−60.68	0.04	5
Sex	0.299	2	−56.72	0.01	37
Null	0.332	1	−53.51	0.00	185

gradient of predation, including stomach contents and predator strategy. Along these dimensions, small snakes separated from intermediate and large ones, with the largest snakes closely associated with underwater foraging for crayfish in river pools (Fig. 2). Small snakes had higher proportions of empty stomachs and were associated with runs and riffles. Those snakes with prey items in their stomachs clustered in areas on the ordination diagrams associated with a more generalist diet in the absence of crayfish.

Prey Items Consumed

Prey mass was available for 46 (26 crayfish and 20 fish) whole prey items. Crayfish ranged in mass from 0.65–2.5 g ($\bar{x}$ = 1.24, s = 0.46), while fish ranged from 0.88–1.9 g ($\bar{x}$ = 1.02, s = 0.55). There was no statistically significant difference between the mass of prey types (t = 0.48, df = 1, P = 0.65); and there was no significant relationship between prey mass and snake SVL (R^2 = 0.06 P = 0.384, Fig. 3), with even the largest snakes consuming small prey.

There was a significant difference in direction of ingestion, whether crayfish or fish (χ^2 = 86.75, df = 67, P < 0.001). We were able to identify 22 of the crayfish as ingested tail-first, while 4 were ingested bent-double. All fish, whether cyprinids or cottids, were ingested head-first.

There was an overall significant difference in the frequency of prey types consumed by snakes (χ^2 = 118.45, df = 5, P < 0.001). Crayfish comprised 56.1% of all prey items (n = 79), while 22.6% were cottid fish (n = 32), 12.1% were cyprinid fish (n = 17), and 9.2% were slugs (n = 13). Snakes <300 mm fed on cyprinid fish (n = 13) and slugs (n = 9). Snakes 301–500 mm had the most diverse diets, feeding on slugs (n = 4), cyprinid (n = 4) and cottid fish (n = 27), and crayfish (n = 6). Snakes >500 mm fed predominately on crayfish (n = 73), and less often on cottid fish (n = 5) (Table 2). The relative abundance of crayfish and cottid fish in each of the 3 stream categories were: riffle (crayfish, 0.14/m^2, cottids 0.28/m^2), run (crayfish, 0.22/m^2, cottids 0.62/m^2), and pool (crayfish, 0.60/m^2, cottids 0.31/m^2). We were unable to assess the relative abundance of either slugs or cyprinid fish.

Foraging Behavior

We were able to classify 41% (n = 110) of the 263 snakes observed to each of the 3 designated foraging behaviors. Overall, there was a significant difference with regard to the observed foraging behaviors of size classes (χ^2 = 44.15, df = 4, P < 0.001). A significantly greater number of snakes <300 mm were observed foraging (sit and wait) within the creek (χ^2 = 13.65, n = 19, 70.3%). These snakes were typically observed coiled atop a rock, with their heads positioned downstream, parallel with the current. Only 5 snakes (18.5%) were observed foraging from shore, their heads facing the creek, and 3 snakes (11.1%) were observed attempting to forage underwater. There was no difference in the
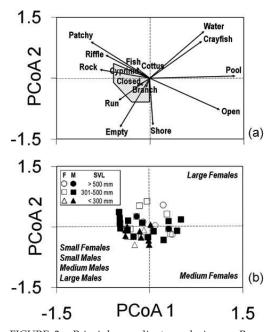
FIGURE 2. Principle coordinate analysis on a Bray-Curtis distance matrix derived from 15 foraging behavior characteristics of *Thamnophis elegans* (n =116) collected at Umtanum Creek, Washington, May through September 2005. The 1st and 2nd axes represent 49% and 17% of the total foraging variability among animals. Plot A shows relationships of environmental variables including position where snakes hunted (shore, branch, rock, and water), forest canopy (open, closed, patchy), river habitat (pool, riffle, run), and stomach contents of snakes (cottus, crayfish, cyprinid, unidentified fish, empty). Shaded area represents the minimum convex polygon drawn around all animals classified as small. Plot B shows positions of individual animals within ordination space. Open symbols are females, closed symbols are male. Circles indicate snakes >500 mm, squares indicate snakes 301–500 mm, and triangles indicate snakes <300 mm. Shaded area represents the minimum complex polygon drawn around all snakes classified as small (SVL<300 mm). Sex-size labels are recorded in the quadrant that contains the average response for that category.

observed foraging behavior within the intermediate size class (301–500 mm). Twelve snakes (28.5%) were observed foraging sit and wait within the creek, 47.6% (*n* = 20) foraged from shore, and 23.8% (*n* = 10) were observed foraging underwater. For snakes >500 mm, a significantly greater number of individuals foraged underwater (χ^2 = 10.58, *n* = 28, 68.2%).

Only 7.3% (*n* = 3) foraged sit and wait within the creek, and 24.3% (*n* = 10) foraged from shore.

Stream Habitat Use

Each of the 3 stream categories were present in nearly equal proportions (riffles = 31.5%, runs = 33.5%, and pools = 35%) along the 1-km stretch of creek surveyed. Stream use, however, differed significantly between size classes (χ^2 = 67.06, *df* = 4, *P* < 0.001) for the 110 snakes for which we had data. Snakes <300 mm foraged significantly more often within runs (χ^2 = 24.94, *n* = 19, 70.3%). Just 18.5% (*n* = 5) foraged in riffles and 11.1% (*n* = 3) in pools. Within the intermediate size class, 61.9% (*n* = 26) were observed in riffles, 26.1% (*n* = 11) in pools, and 11.9% (*n* = 5) in runs. Snakes >500 mm were observed significantly more often in pools (χ^2 = 12.06, *n* = 31, 75.6%), and fewer snakes foraged in riffles (*n* = 8, 19.5%) than in runs (*n* = 2, 4.8%).

DISCUSSION

Our study shows the Umtanum Creek population of *T. elegans* undergoing an ontogenetic shift within size-classes in terms of foraging behavior, diet (Table 2); and for the smallest and largest snakes, microhabitat (stream) usage. Specialization at this level may strongly influence the overall niche variation of a population or species. This effect can be easily overlooked if this level of specialization is not accounted for (Bolnick and others 2003). Snakes <300 mm fed primarily on cyprinid fish, and only occasionally on slugs. Snakes 301–500 mm had the most varied diet, feeding on slugs, cyprinid and cottid fish, and crayfish, but primarily consumed cottid fish. Snakes >500 mm fed nearly exclusively on crayfish, with no other populations of *T. elegans* reported to feed so heavily on crayfish (Fitch 1965; Arnold 1981; Gregory 1984a). Overall, 52.4% of captured snakes contained prey items, which is higher than any previous work on *Thamnophis* spp. (Kephart 1982; Lind and Welsh 1994; Tuttle and Gregory 2009). Other populations of *T. elegans* are known to feed on slugs (Gregory 1978; Arnold 1981), and similar to our study population, slugs are usually consumed by smaller individuals (Farr 1988). The observed shift from predominately vertebrate to invertebrate prey by this popula-
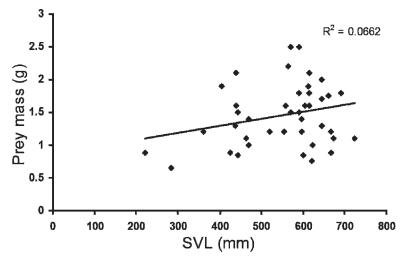
FIGURE 3.   Relationship between the mass of whole prey items and snake SVL ($R^2 = 0.086$, $P = 0.348$) for 3 size classes of *Thamnophis elegans* ($n = 46$) collected at Umtanum Creek, Washington, May through September 2005.

tion is atypical. Most dietary studies on snakes (including *Thamnophis* spp.) show the opposite (Macias-Garcia and Drummond 1988; Greene 1997; Lukose 2000).

Prey items consumed by our study population of *T. elegans* were small in terms of mass ($\bar{x} = 1.13$ g). The largest size class of snakes continued to forage for and consume very small prey items. The largest individual captured, a 723 mm female, contained a single crayfish with a mass of 1.1 g. In some species of snake, as an individual grows larger small prey items are excluded from the diet (Macias-Garcia and Drummond 1988; Holycross and Mackessy 2002; Rodriguez-Robles 2002). Although larger prey items are available at Umtanum Creek, such prey may present snakes with handling and ingesting problems. For example, on one occasion, a large crayfish was observed to

TABLE 2.   Number of prey types ($n = 141$) consumed by 3 size classes (mm SVL) of *Thamnophis elegans* ($n = 138$) collected from May through September 2005 at Umtanum Creek, Kittitas County, Washington.

Prey type	<300	301–500	>500
Crayfish	—	6	73
Cottid fish	—	27	5
Cyprinid fish	13	4	—
Slugs	9	4	—

capture and partially consume an adult male *T. elegans* (Weaver 2004).

Direction of ingestion for crayfish and fish differed. Most vertebrates consume prey head-first (Eisenberg and Leyhausen 1972). Among snakes, several studies have shown that tactile cues such as scale overlap or direction of hair of prey may be used as stimulus for ingestion (Greene 1976; Ashton 2002); however, both prey mass and type influence direction of ingestion (Mori 1991, 1996). Although we did not directly test what factors influence direction of ingestion in this population of *T. elegans*, some differences are evident. Large crayfish may present snakes with significant challenges in terms of ingestion, and even small crayfish possess enlarged chelae (claws) that may harm snakes. By ingesting crayfish tail-first, these appendages are kept away from the head and neck of a snake. Other thamnophiine snakes, such as *Regina* spp., have been observed to ingest crayfish in this manner (Godley 1980). These snakes also primarily consume recently molted crayfish, a phenomenon we observed twice. When ingesting fish, snakes consumed all head-first. Although we did not specifically address this handling behavior, on 3 occasions one of us (REW) observed adult male *T. elegans* attempting to consume cottid fish tail-first along the nearby Yakima River. Despite the vigorous efforts of these snakes, the pronounced pectoral
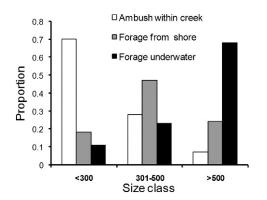
FIGURE 4. Proportion of *Thamnophis elegans* (n = 110) for each size class exhibiting 1 of 3 foraging behaviors at Umtanum Creek, Washington, observed May through September 2005.
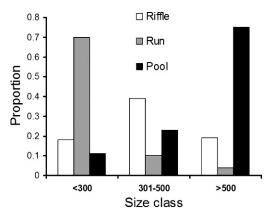

FIGURE 5. Proportion of *Thamnophis elegans* (n = 110) for each size class foraging in 3 stream habitat categories at Umtanum Creek, Washington, observed May through September 2005.

fins of the cottids prevented ingestion. Head-first ingestion, therefore, may allow for easier handling and quicker swallowing of cottid fish.

Our multivariate analysis showed the importance of size in the observed foraging behaviors of individuals in our study population (Table 1). Individuals <300 mm foraged most often from rocks within the creek (Fig. 4) and along runs (Fig. 5). While observing these snakes at the study site, it was apparent that these smaller snakes lacked the consistent ability to submerge and crawl along the creek bottom (small snakes were simply swept away by the current), or dive in pools in a manner similar to larger snakes. This could explain why smaller snakes were not observed foraging in pools as often as larger snakes. This may also explain the lack of crayfish and cottid fish (both are substrate dwelling prey items) in the diet of these smaller individuals. The ability to dive and forage in deep water is characteristic of a repertoire of behaviors shown in other species of *Thamnophis* deemed aquatic specialists (Macias-Garcia and Drummond 1988), or ''obligate'' aquatic specialists (de Queiroz 2003). Juvenile *T. atratus* in northern California (Lind and Welsh 1994) have also shown a similar pattern in stream use.

Snakes we categorized as intermediate in size appear to be generalists in terms of stream usage. These snakes foraged along riffles, runs, and pools (Fig. 5). The largest class of snakes were the most specialized in terms of both prey consumed (crayfish), foraging behavior (forage underwater), and stream use (pools). The ability

of these larger snakes to forage in deep water is most likely the result of an increase in mass and physical development of individual snakes. This has also been documented for *T. atratus* (Lind and Welsh 1994). The high numbers of crayfish in the diet of larger snakes (Table 2), may reflect the abundance of crayfish in pools (0.60/m²) relative to other stream habitat categories, or may be a function of the ability of these snakes to capture, handle, and consume such bulky prey.

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