

Diet and Prey Size of the Flathead Snake, *Tantilla gracilis*

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Diet and prey size relationships of Flathead Snakes (*Tantilla gracilis*) in the pine-hardwood forests of east Texas were determined on 68 individuals. Ninety-five percent of the snakes contained prey of which a large proportion was identifiable. Approximately 80% of the diet (by frequency) of *T. gracilis* consisted of coleopteran (beetle) larvae of the families Alleculidae, Elateridae, and Tenebrionidae. Other prey were centipedes and terrestrial snails. Correlation of prey size with snake size revealed a positive relationship, but accounts for little of the variation. Adults and juveniles ingested the same relative prey sizes with juvenile snakes predominately feeding on alleculid larvae and adults feeding on tenebrionid larvae. Larger snakes had a greater prey mass in their alimentary tracts; however, they did not consume significantly greater numbers of prey items. Direction of prey ingestion was primarily posterior first (72%). Because most of their prey have elongated bodies, it appears that *T. gracilis* responds to growth changes in body size by switching to different prey types. Choosing prey by size may be less important than prey shape for *T. gracilis* because of the morphological adaptations associated with a fossorial existence.

A fundamental question of snake foraging ecology is what do they eat (Shine, 1977; Greene, 1997)? Mushinsky's (1987) review of this topic revealed that there are still many species for which we lack basic dietary information. Much of this absence derives from the complications of studying snake foraging ecology (e.g., small sample sizes, highly efficient digestive tracts, and infrequent feeding; Godley et al., 1984). The dietary literature of snakes has progressed from describing types of prey, to representing prey types as a function of snake size, to finally relating prey sizes to snake size (Arnold, 1993). A number of studies addressing this latter approach have found a positive relationship between prey size and snake size (for review see Arnold, 1993); however, many of these relationships are weak. Some exceptions finding prey size to be strongly influenced by snake size are Plummer and Goy (1984) and Greene et al., (1994), whereas others such as Shine (1977, 1987) and Garcia and Drummond (1988) reported little or no size relationship. Reasons for the variations in size relationships have been reviewed by Shine (1991), Arnold (1993), and Greene (1997).

Flathead Snakes (*Tantilla gracilis*) are small fossorial opisthoglyphous colubrids found throughout the mid-southwestern United States (Wright and Wright, 1957). Although rarely observed because of their burrowing habits, these snakes are common throughout much of their range (Force, 1935; Tennant, 1984). Limited ecological studies of *T. gracilis*, include those by Strecker (1926), Force (1930, 1935), Clark

(1967), Roberson (1980), and Cobb (1990). The most thorough study (Force, 1935), detailing much of the natural history of *T. gracilis*, included anecdotes of prey type (described as "centipedes and earth-dwelling insect larvae"). In this paper, I describe various aspects of the feeding ecology of *T. gracilis* in the pine-hardwood forest of east Texas. Goals of this study were (1) to describe the types and proportions of prey eaten in regard to snake size and (2) to examine the relationships of prey type and size as a function of snake size.

MATERIALS AND METHODS

Tantilla gracilis was collected in similar habitats from three localities in adjacent Smith and Henderson Counties in northeastern Texas. I hand-captured 68 *T. gracilis* during daylight hours on rocky hillsides in mixed pine-hardwood forests. I located snakes either on top of the soil or underneath stones (8–60 cm in diameter), from March through October 1988. All snakes were sacrificed using chloroform within six hours of capture, preserved in 10% formalin, and stored in 70% ethanol. Specimens were deposited in the University of Texas at Tyler Vertebrate Collection. I determined snake sex by the presence or absence of hemipenes or by observation of the gonads during dissection. Positive sex identification was not possible for some of the smaller individuals; thus, I classified snakes of 100 mm or less snout-vent length (SVL) as juveniles, a size corresponding to the estimated size of sexual maturity for *T. gracilis*

TABLE 1. SNOUT-VENT LENGTH (SVL), BODY MASS (BM), MIDBODY DIAMETER (MBD), HEAD WIDTH (HW), HEAD LENGTH (HL), JAW LENGTH (JL), AND NUMBER OF PREY PER SNAKE (NPS) FOR ADULT MALE ($n = 30$), ADULT FEMALE ($n = 12$), AND JUVENILE ($n = 26$) *Tantilla gracilis*. All data are reported as means \pm 1 SD with ranges in parentheses.

	Males	Females	Juveniles
SVL (mm)	126.3 \pm 13.80 (103–151)	141.4 \pm 20.99 (112–172)	85.5 \pm 9.56 (61–98)
BM (g)	1.46 \pm 0.39 (0.78–2.30)	1.85 \pm 1.06 (0.76–4.32)	0.57 \pm 0.16 (0.23–0.83)
MBD (mm)	4.2 \pm 0.41 (3.40–4.97)	4.26 \pm 0.84 (2.35–5.32)	3.22 \pm 0.45 (2.29–4.15)
HW (mm)	3.95 \pm 0.25 (3.44–4.36)	4.08 \pm 0.42 (3.53–4.79)	3.35 \pm 0.16 (3.00–3.73)
HL (mm)	5.02 \pm 0.31 (4.43–5.56)	5.09 \pm 0.45 (4.60–5.85)	4.28 \pm 0.15 (3.94–4.58)
JL (mm)	5.58 \pm 0.31 (5.00–6.05)	5.67 \pm 0.47 (5.17–6.48)	4.81 \pm 0.15 (4.47–5.13)
NPS	2.5 \pm 1.67 (1–5)	2.8 \pm 1.85 (0–6)	1.9 \pm 1.29 (0–5)

(Force, 1935; Roberson, 1980). I measured snake mass and SVL from live or recently sacrificed individuals, whereas head width, head length, jaw length, and midbody diameter were taken after preservation. Head width was measured at the point of articulation of the mandible and quadrate bones. Head length was measured from the medial and dorsal point above the jaw articulation to the tip of the snout. I calculated jaw length as the length of the hypotenuse of the head length and half the head width (Pough and Groves, 1983). During dissection, I recorded the number and location (stomach or intestine) of prey. To determine the orientation during ingestion, I only examined relatively intact prey within the stomach. Prey items were removed and stored in 70% ethanol. Prey measurements of body length, body width, and head width were taken using a calibrated light microscope. I measured dry prey masses for each snake after filtering alimentary tract contents onto filter paper attached to a vacuum and oven-drying for 24 h at 42 C.

Partially digested prey were identified from their undigested chitinous body parts (i.e., heads, mandibles, and body segments). I identified coleopteran larvae to family following Boving and Craighead (1931) and Peterson (1960) and centipedes and snails to order using Barnes (1987).

Statistical analyses were conducted with SPSS Version 7.5 (SPSS, Inc., Chicago, IL, 1997, unpublished). Abbreviations used for morphological variables are snout-vent length (SVL), midbody diameter (MBD), snake head width (SHW), snake head length (SHL), snake jaw length (SJL), prey head width (PHW), prey body width (PBW), and prey body length (PBL).

RESULTS

Females, males, and juveniles were significantly different for all morphometric variables

(Table 1; Kruskal-Wallis; SVL $H = 48.9$, BM $H = 46.4$, MBD $H = 36.2$, HL $H = 46.3$, HW $H = 44.4$, JL $H = 46.2$; $P \leq 0.001$). Adult females and adult males were not significantly different for most body measurements (Mann-Whitney; BM $Z = -0.515$, MBD $Z = -0.348$, HL $Z = -0.251$, HW $Z = -0.585$, and JL $Z = -0.362$; $P \leq 0.05$); however, for SVL, females were longer than males (Mann-Whitney $Z = -1.895$; $P = 0.058$). Further comparisons of adult males and females using SVL as a covariate revealed that females had a larger body mass but did not differ from males in the measurements of MBD, HL, HW, HL, and JL. Reproductive condition was not accounted for in these analyses, but vitellogenic and gravid females would be expected to have a larger body mass.

Of 68 snakes, 65 (95.6%) had food in their alimentary tracts and a total of 158 individual prey items were found resulting in a mean of 2.4 prey per snake. *Tantilla gracilis* fed exclusively on coleopteran larvae of the families Alleculidae, Elateridae, and Tenebrionidae, centipedes (orders Lithobiomorpha and Scolopendromorpha), and snails (order Stylommatophora; Table 2). Most snakes ($n = 46$) contained multiple prey distributed as follows: 19 of 65 snakes had two prey, 14 snakes had three prey, seven snakes had four prey, five snakes had five prey, and one adult female (SVL = 159 mm) had six prey. Seventy-two percent of 43 intact prey from 23 snakes were ingested posterior first. For 44 snakes, 35 with prey in the stomach and 37 with prey in the intestine, the locations of 125 prey were equally distributed in the stomach (49.6%) and intestine (50.4%). Small nematodes found in a few of the snakes were most likely parasites of beetle larvae and centipedes (Force, 1935). Occasional sand granules found in the digested remains were considered to have been secondarily or incidentally ingested.

Snake body size characteristics were not

TABLE 2. PREY IN THE ALIMENTARY TRACT OF *Tantilla gracilis*. Some snakes had more than one type of prey; therefore the numbers of snakes and prey are unequal.

Snake status	Proportion and number of snakes with prey						Unidentified prey item	n
	Tenebrionidae	Elateridae	Alleculidae	Unidentified coleopteran larvae	Total larvae	Centipede	Snail	
Juvenile (n = 24)	16.0% (8)	10.0% (5)	50.0% (25)	4.0% (2)	80.0% (40)	16.0% (8)	0.0% (0)	4.0% (2)
Male (n = 30)	59.5% (44)	10.8% (8)	10.8% (8)	2.7% (2)	83.3% (62)	10.8% (8)	2.7% (2)	2.7% (2)
Female (n = 11)	44.8% (22)	11.7% (4)	2.9% (1)	2.9% (1)	82.3% (28)	6.0% (2)	11.7% (4)	0.0% (0)
Total (n = 65)	46.8% (74)	10.8% (17)	21.5% (34)	3.2% (5)	82.3% (130)	11.4% (18)	3.8% (6)	2.5% (4)

strongly correlated with prey size and likely resulted from prey type differences in relation to snake size. Juvenile snakes primarily fed on alleculid larvae, whereas, the majority of prey eaten by adults were tenebrionid larvae (Table 2). Although two adult individuals revealed that the upper limit of prey size has the potential to increase sharply, the remaining 39 adult snakes continued to feed upon small prey.

Simple regression of PHW against SHW and PHW against SVL weakly showed that larger *T. gracilis* ate larger diameter prey (SHW: $r^2 = 0.10$, $P \geq 0.01$, $n = 65$; SVL: $r^2 = 0.10$, $P \leq 0.01$). Correlation of PBW against snake mass revealed a pattern similar to other morphological comparisons. However, when PHW was compared between juvenile (mean = 1.2 ± 0.38 mm) and adult snakes (mean = 1.5 ± 0.45 mm), juvenile snakes consumed smaller prey ($P \leq 0.05$, $F = 4.39$, ANOVA). I regressed PHW against SHW and plotted the resulting residuals against SVL. No relationship existed ($r^2 = 0$), indicating adult and juvenile snakes consumed the same relative sizes of prey. Longer snakes contained greater prey masses ($r^2 = 0.36$, $P \leq 0.01$, $n = 65$) but did not eat greater numbers of prey ($r^2 = 0.03$, $P \geq 0.1$, $n = 65$). Regression of PBL against all snake size variables indicated that larger snakes did appear to eat longer prey (ranges for r^2 were 0.16–0.37; $n = 20$), albeit $P = 0.077$ and 0.069 for SVL and SHW, respectively. The upper limit of PBL in these regressions rose sharply (more so than with PHW), yet individuals continued to eat smaller prey.

DISCUSSION

In this study, *T. gracilis* fed upon beetle larvae, centipedes, and occasionally terrestrial snails. These findings generally are consistent with Force (1935) and (Roberson, 1980), although there are some interesting differences. In the stomachs of 73 *T. gracilis* from Kansas, Force found mycetophilid, noctuid, and tipulid larvae all of which are considerably more malleable in texture than coleopteran larvae identified in this study. Force also noted that captive *T. gracilis* would eat pyrochroid larvae and earthworms. Diet composition sampled by Roberson (1980) in Missouri was identical to Force (1935) but included lepidopteran larvae. Such dietary variation in this study was not evident; rather coleopteran larvae of three families (Alleculidae, Elateridae, and Tenebrionidae) dominated the diet of *T. gracilis* in the mixed pine-hardwood forests of East Texas. Diets of other *Tantilla* species exhibit similar prey. For example, Hamilton and Pollack (1956) noted that *Tantilla*

coronata fed mainly upon centipedes, sometimes eating blattids, coleopteran larvae, and millipedes. Lindner (1962) found that *Tantilla atriceps* in Arizona fed entirely on coleopteran and lepidopteran larvae. Smith (1982) found that *Tantilla relicta* in Florida fed primarily on tenebrionid larvae, occasionally on centipedes and snails, similar to this study. Thus, it appears that *Tantilla* choose to feed on elongated invertebrate prey.

Shine (1986) summarized the proportion of snakes containing food for a number of species. In general, about 50% of snakes contained food; however, extremes existed at both ends of the spectrum, with considerable variation in some species. In this study, 94% of *T. gracilis* had identifiable prey in their alimentary tracts. Other studies of *T. gracilis* showed 86% (Force, 1935) and 73% (Roberson, 1980) to have identifiable prey. Smith (1982) found identifiable prey in 57% *T. relicta*. Shine (1986) suggested that feeding rates of snakes may be positively correlated with and potentially reflect their metabolic requirements. The combination of prey in large proportions (many intact) and small body size in *Tantilla* suggests a high metabolic requirement. Nevertheless, the lack of data on *Tantilla* metabolic rate and prey abundance make it difficult to link causative factors to metabolic requirements.

Snake diets sometimes exhibit ontogenetic change (Mushinsky et al., 1982; Lind and Welsh, 1994; Greene, 1997). The ontogenetic shift in *T. gracilis* from alleculid larvae to tenebrionid larvae is evident in this study. Force (1935) also found that juvenile *T. gracilis* fed on mycetophilid larvae while adults fed on coleopteran larvae and centipedes. Because of the dominance of one prey type among the diversity eaten by both adults and juveniles, it initially appears that snakes select prey primarily according to type. However, because prey type differs between large and small *T. gracilis*, there is the indication that prey choice is possibly important in structuring the size relations (Shine, 1991) between *T. gracilis* and its prey.

Although there was a distinct ontogenetic shift in prey type, predator-prey size relationships in this study were only weakly correlated. Review of this relationship by Arnold (1993) indicated the general trend for several snake species is to increase prey size with increased snake size. However, these snake-prey relationships are often weakly correlated because large adults occasionally eat small prey, in addition to larger prey (Shine, 1977; Godley, 1980; Greene, 1984). Similarly for snakes with multiple prey, if prey size per snake is averaged and plotted against

snake size, low positive correlations are observed (see *T. gracilis* data in Arnold, 1993). Obviously, some of the variation in these weak relationships of prey size against snake size represents changes in prey type. Another explanation is prey size, where small snakes may not be able to handle relatively large prey compared to larger snakes (Pough and Groves, 1983). For example, Pough (1977) showed that larger *Thamnophis sirtalis* could ingest relatively larger prey than smaller conspecifics. Nevertheless, if snakes choose prey that are relatively large, which would be the most profitable energetically (Arnold, 1983, 1993), strong correlations should exist between predator size and prey size as long as the energetics of foraging time and handling time is not compromised (Schoener, 1971). However, Shine (1991) showed that, because many adults continue to eat small prey, strong correlations are observed regarding maximal prey size but not minimal prey size, described as a telescoping pattern in Arnold (1993). Without data on prey availability and experimental feeding trials such as those by Shine (1991) or Webb and Shine (1993), it is difficult to detect the causal basis for the predator-prey size relationships.

The predator-prey size relationships in this study, showed that *T. gracilis* did exhibit a telescoping pattern and that adults and juveniles consumed prey of the same relative sizes. Greene (1984) has shown the potential for such a relationship to be influenced by overall prey body shape. Greene found the diet of *Micrurus fulvius* (a predominately ophiphagous snake) to be more closely associated with prey length, which kept relative prey diameters similar. Because of their apparent preference for elongated invertebrates, *T. gracilis* may follow a similar pattern as *M. fulvius*. One possible correlate to this proposed similarity may lie in skull morphology (Pough and Grove, 1983). As indicated by Savitsky (1983) and Greene (1984), both *M. fulvius* and *Tantilla* have morphological adaptations such as reduced scale numbers, fused cephalic scales, and shortened quadrate and mandibular bones which limit head width and gape size. These adaptations do not allow a large range in prey size, but those snakes feeding on elongated prey would be circumventing possible prey diameter restrictions.

One factor this study did not address was the potential influence of prey availability. I propose the diet of *T. gracilis* is a reflection of prey selection rather than prey availability. Both Kephart and Arnold (1982) and Gregory (1984) have shown the availability of prey to influence diet; however, in general neither were speaking

in reference to prey size or shape. I acknowledge that most likely the specific prey in this study are to some degree a reflection of the prey availability (e.g., the preponderance of coleopterans) but overall that prey size and shape are the more determinate factors. Although I did not sample the subterranean habitat for prey availability, a wide variety of other arthropods were observed and were presumably available as prey.

In conclusion, *T. gracilis* was an effective model for examining prey size relationships, because a high percentage of individuals had food in their digestive tracts consisting exclusively of invertebrates with hard chitinous body parts rendering prey size easily measured. *Tantilla gracilis* specialized in prey selection and ate prey similar to other *Tantilla* species. Feeding rates were high, and an ontogenetic dietary shift in prey type was evident; yet both juveniles and adults consumed the same relative size of prey. Head morphology likely limits the gape size of *Tantilla* and possibly has resulted in the selection of elongated prey. The combination of the morphological constraints and prey selection led to the observed low correlations between snake size and prey size. Further investigations on prey specialization and size relationships should consider identifying possible trends between morphological adaptations associated with a specific type of existence (e.g., fossorial), prey shape, and prey availability.

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