

Plasticity of Foraging Behavior in Garter Snakes (*Thamnophis sirtalis*) Reared on Different Diets

Gordon M. Burghardt and Mark A. Krause
University of Tennessee, Knoxville

The ontogeny of foraging was studied in 107 neonatal garter snakes (*Thamnophis sirtalis*) reared on 3 different diets: fish, leafworms, or mixed. Times to approach, capture, handle, and swallow prey were measured during each snake's first feeding and again after 11 to 12 meals. Overall times to consume prey decreased between the first and last tests for the 3 groups, but both prey type and the relative amounts of prey consumed differentially affected the various feeding phases. Approach latencies significantly decreased for snakes fed worms or fish exclusively but not for the mixed-diet snakes. The degrees to which capturing and swallowing latencies decreased differed among diet groups. Diet had little effect on prey handling duration. Sex and litter effects were reduced after feeding experience. These results reveal flexibility in feeding behavior as well as the costs and benefits of experience with multiple prey classes.

Locating and consuming prey are vital aspects of behavior in actively foraging animals. Successful predation depends on an animal's ability to detect, capture, handle, and ingest its prey. Most predators have evolved adaptations for prey detection, such as search strategies, as well as adaptations for capturing and handling prey, such as increased motor skills. The time and energy spent to complete the various phases of predation may vary according to not only the size or species of prey but also the experience, maturation, and size of the predator.

Improvements in foraging ability, namely prey detection and handling, have been examined in many vertebrates, including birds (Marchetti & Price, 1989; Yoerg, 1994), fish (Croy & Hughes, 1991a, 1991b), and squamate reptiles (de Queiroz & de Queiroz, 1987; Halloy & Burghardt, 1990; Mori, 1991, 1996). Even in insects, experience and learning may play unexpectedly important roles (e.g., Kral, 1998). How animals incorporate information into their feeding strategies has received considerable theoretical attention (Stephens & Krebs, 1986), although individual differences in developmental patterns are rarely considered in such models. The effects of experience on development and adult

behavior are in need of closer examination. Predictions of adult foraging behavior can be improved when the effects of ontogenetic factors are considered (Yoerg, 1994).

Ecologists often distinguish between dietary generalists and specialists (Morse, 1980). Specialist predators typically show behavioral and morphological traits conducive to foraging successfully on fairly specific prey types. Predatory generalists, in contrast, consume a wider variety of prey types and, consequently, are less likely to evince such specialized traits, especially without extensive experience. Even precocial predators with no parental care, such as many squamate reptiles, show improvements in foraging ability with experience and age (Burghardt, 1978; Halloy & Burghardt, 1990; Mori, 1991, 1996) and indeed have an often overlooked capacity to learn (Burghardt, 1977).

Improvements in foraging abilities may include shifts in prey selection when body size constraints are removed (Arnold, 1993), the development of increased efficiency for handling a given type of prey, or both. For example, Halloy and Burghardt (1990) showed that neonatal common garter snakes (*Thamnophis sirtalis*), a dietary generalist, are less adept at various aspects of fish handling in comparison with neonatal *Thamnophis melanogaster*, an aquatic prey specialist. In fact, the detection and capture of aquatic prey by *Thamnophis melanogaster* is typically superior to that of *Thamnophis sirtalis* (Drummond, 1983), although adult *Thamnophis sirtalis* that have experience with feeding on fish show comparable prey handling abilities to those of adult *Thamnophis melanogaster*. Similarly, rat snakes (*Elaphe climacophora*), which specialize in preying on rodents, show superior prey handling abilities as hatchlings compared with *Elaphe quadrivirgata*, a dietary generalist (Mori, 1996). However, yearling and juvenile *Elaphe quadrivirgata* with rodent feeding experience are nearly equal in rodent handling ability to *Elaphe climacophora*. These results suggest that experience plays a crucial role in the development of prey handling skills in generalist snake predators.

Thamnophis sirtalis, the most widely distributed snake in

Gordon M. Burghardt, Departments of Psychology and Ecology and Evolutionary Biology, University of Tennessee, Knoxville; Mark A. Krause, Department of Psychology, University of Tennessee, Knoxville.

This research was supported by Grant IBN 94-11140 from the National Science Foundation.

We sincerely thank Paul Andreadis, Mark Waters, Matt Lanier, and Casey Newton for their comments on an earlier version of this article; Barbara Manzer for her assistance with animal care; and Jim Gillingham and the staff and the students at the Central Michigan University, Beaver Island Biological Station. Roger Hughes provided valuable suggestions for improving this article.

Correspondence concerning this article should be addressed to Gordon M. Burghardt, Department of Psychology, University of Tennessee, Knoxville, 307 Austin Peay Building, Knoxville, Tennessee 37996-0900. Electronic mail may be sent to gburghar@utk.edu.

North America, consumes a wide variety of both terrestrial and aquatic prey, including fish, earthworms, leeches, adult and larval amphibians, mammals, and occasionally birds (Fitch, 1965; Rossman, Ford, & Seigel, 1996). Prey availability and neonatal responses to prey vary across the geographic range of *Thamnophis sirtalis* (Arnold, 1992; Burghardt & Schwartz, 1999). However, this species often shows strong predatory and chemoreceptive responses to prey not found in source populations. This may be among the explanations for the apparent success of *Thamnophis sirtalis* in invading new habitats and its widespread geographic distribution. Although experience may contribute to the development of foraging skills in this species, the extent of plasticity may vary with the type of prey involved, the phase in the foraging sequence, and genetic variation. Furthermore, it is not obvious to what extent the skills acquired in dealing with one prey type transfer to other prey classes. In this study, we measured the degree to which neonatal garter snakes become more capable foragers with feeding experience and how specific types of prey (fish and worms) may differentially influence the development of prey consumption. We also sought to determine which phases of the predation sequence (detecting, capturing, handling, and swallowing) are most influenced by feeding experience. By using many different litters from one population, we controlled for between-family genetic variation.

All snakes that were tested were neonates born to mothers collected from an insular population in which the natural diets of the snakes from the sampled population consisted almost exclusively of earthworms. To date, there are no records of garter snakes anywhere on the island consuming fish (Gillingham, 1988), and the locale sampled here had no ponds or streams. We hypothesized that (a) because the garter snake is a generalist predator, prey handling would improve with experience for both prey types in neonatal garter snakes, especially for prey that seemed more difficult to handle (i.e., fish); (b) the relative amounts of each prey type consumed would differentially influence the development of feeding efficiency; and (c) various prey characteristics (morphological and behavioral) would lead to differences in prey consumption times among snakes fed either prey type. We also evaluated sex and litter differences because of the substantial evidence that family, but not sex, contributes to individual differences in chemosensory prey responses (Arnold, 1981; Burghardt & Schwartz, 1999).

Method

Subjects

A total of 191 neonatal garter snakes (*Thamnophis sirtalis*) from 30 litters (mean litter size = 6.4, range = 2–14) were tested. The neonates were born to mothers collected at a 2 hectare field on Beaver Island in Lake Michigan. At birth, all neonates were housed individually in identical clear plastic cages (13.5 × 18.5 × 4.0 cm) that included a paperboard substrate and shelter and a water dish. The snakes were kept at an approximate room temperature of 25 °C, with 30% relative humidity, and on a 12:12-hr light–dark cycle.

Procedure

Neonates were weighed, sexed, measured (snout-vent length [SVL] in millimeters), and assigned to diets of mosquito fish (*Gambusia affinis*; F group: $n = 72$), leafworms (*Lumbricus rubellus*; W group: $n = 70$), or a combination of the two (FW group: $n = 49$). At 14 and 17 days of age, before the feeding tests, all snakes were tested for responses to prey chemicals as part of another study. Two feeding test sessions were then conducted: the first at 19 days of age and the second at 80 days of age. Each snake was offered its first prey on the first test session. At least two separate trials (spaced 2 days apart) were completed at each test session. All trials were videotaped with a hi-8 camcorder (Sony CRD-VX3). If a snake refused to eat on one or both of the trials during each session, a third attempt was made so as to obtain at least one recording. The data reported below are for the first videotaped trial of each session in which the snakes ate. Snakes in the FW group were always fed fish on the first trial and worms on the second trial within each test session (this study was part of a larger project requiring that the snakes in each treatment be exposed to identical environmental conditions). The data reported below are for snakes that ate at least once during both test sessions if they were placed on diets of single prey items. Data on the FW group are reported for snakes that ate both prey types during each test session. Eighty-four snakes were dropped from the analyses because of mortality occurring between test sessions ($n = 31$), small litter sizes (<4 snakes per litter; $n = 31$), or refusal to eat during testing ($n = 22$), bringing the total sample size to 107 snakes (F group: $n = 40$, W group: $n = 47$, and FW group: $n = 20$) from 18 litters.

Testing took place in an environmental chamber (2.5 × 1.6 × 2.1 m) with an air temperature kept at approximately 25 °C. Live prey items, weighed to within 10%–15% of each snake's body weight, were placed in petri dishes in the center of each snake's home cage for each 1-hr test session. Water and a shallow layer of dirt were placed in each dish for fish and worms, respectively. An observer videotaped all trials and remained in the chamber to take as much data as possible by hand. The prey were removed if the snakes refused to eat by the end of each test session. For 6 weeks after the first test session, the snakes were fed to satiation twice weekly on their designated diets. After 11–12 feedings, they were tested again following the same method used in the first test session. Table 1 lists and defines the dependent measures taken during each test session. In addition to recording the durations of various consumption phases, descriptive measures were recorded, including prey capture locations, the directions in which prey were swallowed, and the number of times prey were dropped. This allowed assessment of any qualitative differences in prey handling.

Table 1
Dependent Measures Used for Each Feeding Test

Measure	Definition
Approach latency	Number of seconds from start of trial to time snake's head crossed rim of dish
Capture time	Number of seconds from approach latency to final prey seizure
Handling time	Number of seconds from prey seizure to onset of prey swallowing
Swallowing time	Number of seconds from onset of swallowing to first postingestive tongue flick
Total consumption time	Number of seconds from onset of capture to first postingestive tongue flick

Statistical Analyses

We compared data on growth (body weight in grams and SVL in millimeters) between the sexes and among the three diet groups at birth and at 2.5 months of age by using separate one-way analyses of variance (ANOVAs). We performed tests for changes in total consumption times by the F and W groups with a repeated measures general linear model, with the first and last tests treated as within-subjects repeated variables and diet (fish or worms), sex, and litter treated as between-subjects variables. We used a multivariate analysis of variance to test for the effects of diet, litter, and sex on each consumption phase and test session. Because of the small size of the FW group, this group was not included in these multivariate analyses. Five snakes in the W group had excessively long capture times on the last test. These 5 snakes were dropped from the analyses because they were identified as extremes (beyond three standard deviations from the mean) in the Explore function of SPSS (1997). This reduced the sample size for the W group to 42.

We tested changes in total consumption times for the FW group by using paired *t* tests. Within-subjects changes in approach latencies and capturing, handling, and swallowing times were tested with paired *t* tests for each diet group. The number of trials in which snakes dropped prey were compared across the two test sessions by using McNemar tests, and between-diet-group comparisons were made with Mann-Whitney *U* tests. The body regions where prey items were captured and the directions in which prey were swallowed were compared by using Cochran's *Q* and chi-square test statistics.

Changes in total consumption times and in each prey consumption phase were compared between the three diet groups. To do this, difference scores were calculated by subtracting the duration of each phase at the first test from that at the last test. These numbers were then compared using one-way ANOVAs with diet as the between-subjects variable. Tukey's honestly significant difference test was used for all post hoc comparisons. All prey consumption data were natural log transformed ($\ln + 1$) to meet assumptions of normality and homoscedasticity of variances. Alpha values for all statistical tests were set at .05.

Results

Diet differentially influenced the snakes' growth rates, as well as the degree to which prey consumption improved with experience. Effects of sex and litter on growth rates and prey consumption abilities were found. The following results first present data on growth rates as a function of sex and diet. Overall changes as a function of diet are then presented, followed by sections covering the effects of diet on the phases that comprise prey consumption.

Growth

At birth, there were no significant differences between the sexes in either body weight or SVL. There were also no differences in body weight or SVL among the snakes assigned to the three diet conditions. However, at 2.5 months of age, body weights differed significantly among the three diet groups, $F(2, 99) = 26.46, p = .0001$, as did SVLs, $F(2, 80) = 6.73, p = .002$. Figure 1 shows the average body weights (upper panel) and SVLs (lower panel) for all three groups at birth and at 2.5 months. Post hoc comparisons

revealed greater increases in body weight ($p = .0001$) and SVL ($p = .007$) for the W and FW groups than for the F group. Feeding records, which included all food consumed since birth, revealed that snakes from all groups consumed nearly equal percentages of each prey type: for the F group, 97% of the total fish offered, $M = 26.4$ fish per snake; for the W group, 91% of the total worms offered, $M = 22.3$ worms per snake; and for the FW group, 92% of the total fish offered, $M = 13.9$ fish per snake, and 93% of the total worms offered, $M = 15.6$ worms per snake.

At 2.5 months of age, there were no significant differences between the sexes in SVL, $F(1, 81) = 0.89, p = .349$ (for males, $M = 175.3$ mm, $SE = 2.1$ mm; for females, $M = 178.2$ mm, $SE = 2.3$ mm), but females outweighed males, $F(1, 100) = 5.91, p = .017$ (for males, $M = 3.1$ g, $SE = 0.1$ g; for females, $M = 3.4$ g, $SE = 0.1$ g). Both sexes consumed similar percentages of each prey type (males: fish, 95%, and worms, 89%; females: fish, 97%, and worms, 93%). Because body weight and SVL can influence snakes' prey handling ability, body size variables were correlated separately for each sex with the total times to consume prey and each consumption phase for both tests. No significant correlations were found between body weight or SVL and any of the prey consumption phases for either test session or sex.

Changes in Total Prey Consumption Times

The decreases in total consumption times for each group at the first and last test sessions were often dramatic (see Figure 2). To compare changes in total consumption times across the three diet groups, difference scores for each snake were computed by subtracting the total time of the later feeding from the total time of the first feeding. The differences among the groups were not significant, $F(3, 118) = 2.45, p = .067$. However, a significant difference ($p = .042$) was found in response to worms between the W and FW groups (for the W group, mean difference score = 367.7 s, $SE = 65.9$ s; for the FW group, mean difference score = 222.7 s, $SE = 167.4$ s).

The percentage decreases in total consumption times for the three diet groups are shown in Table 2. The W group's average decrease in total consumption time was 74%, whereas the FW group showed only a 40% decrease for worm consumption times. Decreases in consumption time for fish were about 70% for both the F and FW groups (see the "Total time" phase in Table 2). Significant decreases in total prey consumption times were found between the first and last tests, $F(1, 23) = 120.86, p = .0001$, for both the F and W groups. The degrees to which consumption times decreased for either prey were statistically equal, as shown by a nonsignificant interaction between test time and diet, $F(1, 23) = 1.25, p = .276$ (see Table 2).

There were no main effects for litter or sex. However, there was a significant interaction between sex and diet, $F(1, 23) = 5.38, p = .03$. Figure 3 shows differences between the diet groups (F and W, respectively) and sexes in the mean decrease in prey consumption times. At the first feeding,

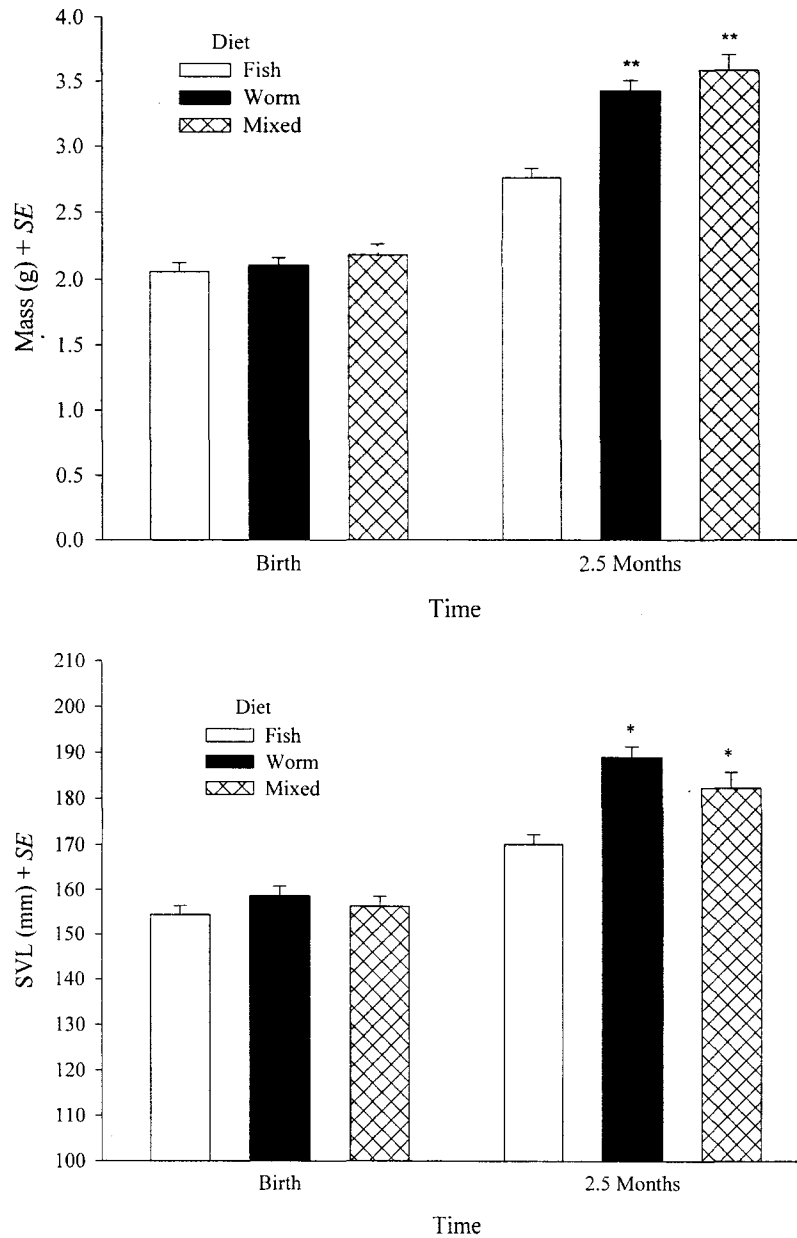


Figure 1. (Top panel) Mean (+SE) body weights for the garter snakes in the three diet groups at birth and at 2.5 months. (Bottom panel) Mean (+SE) snout-vent length (SVL) for the garter snakes in the three diet groups at birth and at 2.5 months. * $p < .01$ represents significant SVL differences at 2.5 months for the garter snakes in the worm and mixed-diet groups compared with those in the fish group. ** $p < .001$ represents significantly higher body weights of the garter snakes in the worm and mixed-diet groups compared with those in the fish group.

females took longer than males to consume fish. However, on the last test, females consumed fish more rapidly than males. Males and females in the W group showed nearly equal consumption times on the first and last tests. A four-way interaction was also found between test session, diet, sex, and litter, $F(8, 23) = 3.57$, $p = .008$. This interaction was explored further by separately testing the diet, sex, and litter variables against each test session. A significant interaction between diet, sex, and litter was found

for the total consumption times on the first test session, $F(8, 58) = 2.99$, $p = .019$. However, this interaction was not statistically significant on the last test session, $F(8, 58) = 1.21$, $p = .337$.

The 20 snakes in the FW group significantly decreased their fish consumption times, $t(19) = 3.93$, $p = .001$, but worm consumption times did not decrease significantly, $t(19) = 1.33$, $p = .199$. Total decreases in consumption times did not differ between the sexes for either prey type.

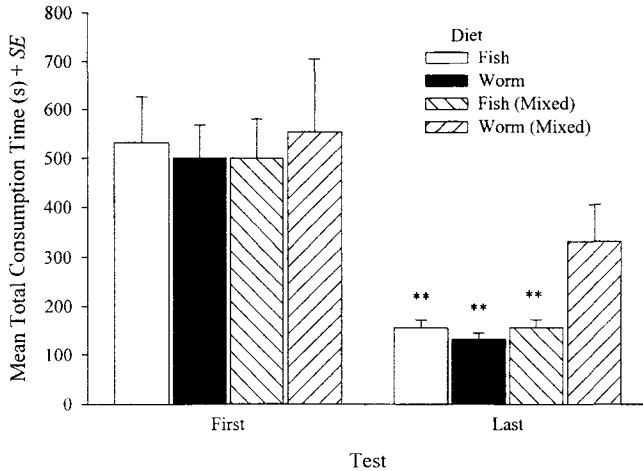


Figure 2. Mean (+SE) total prey consumption times for the garter snakes in the three diet groups on the first and last tests. ** $p < .001$ represents significant decreases in total consumption times between the first and last tests.

Comparisons for Each Feeding Phase

Approach latencies. Figure 4 shows the average approach latencies for each group for both the first and last tests. There was no significant difference between the F and FW groups in their approach latencies to fish on the first test, $t(58) = 1.25, p = .218$, although there was a significant difference between the W and FW groups in their approach latencies on their first tests to worms, $t(60) = 3.95, p = .001$. It should be noted that whereas worms were the first prey

offered to the W group, fish were offered to the FW group before the initial test with worms.

Diet had a significant effect on the changes in approach latencies between the first and last tests, $F(3, 118) = 4.12, p = .008$. Post hoc comparisons revealed a significant difference ($p = .009$) in the reduction in approach latencies between the F group ($M = 490.0$ s, $SE = 112.9$ s) and the FW group when tested on worms ($M = -52.1$ s, $SE = 179.2$ s). The latter group actually showed an average increase in approach latency between the first and last tests (see Table 2).

Within-group tests revealed significant decreases in approach latencies between the two tests for both the F group, $t(39) = 7.23, p = .0001$, and the W group, $t(41) = 4.29, p = .0001$ (see Table 2). Unlike snakes fed on single prey items, snakes in the FW group did not show significant decreases in approach latencies to either fish, $t(19) = 1.39, p = .181$, or worms, $t(19) = -0.40, p = .696$. There was a significant litter effect, $F(17, 58) = 3.36, p = .004$, for approach latency on the first test, but this effect was absent on the last test, and there were no sex differences on either test.

Prey capture. There were no significant effects among the groups for capture times, $F(3, 118) = 1.40, p = .245$. However, of the three phases that comprised total consumption times, capture times showed the greatest decrease from the first to last tests for all three diet groups. Thus, the improved foraging ability appears to be due primarily to an increased ability to capture prey following approach. Changes in capture times were fairly similar among the F, W, and FW groups when tested on fish (see Figure 5 and Table 2). Significant decreases between the first and last tests were found for the F group, $t(39) = 4.65, p = .0001$; the W group,

Table 2
Mean (\pm SE) Times for Each Prey Consumption Phase and Percentage Decreases for the First and Last Tests for Each Diet Group

Phase	Test	F		W		FW-F		FW-W ^a	
		M	(SE)	M	(SE)	M	(SE)	M	(SE)
Approach	First	658.5	(110.3)	910.1	(120.7)	409.8	(103.9)	276.7	(87.7)
	Last	168.5	(51.8)	362.2	(83.1)	284.9	(103.0)	328.8	(159.7)
	% decrease	74.4**		60.2**		30.5		-18.8	
Capture	First	365.3	(96.7)	334.5	(71.2)	359.5	(83.2)	427.8	(143.5)
	Last	44.3	(9.1)	52.1	(10.8)	66.2	(16.7)	231.1	(73.5)
	% decrease	87.9**		84.7**		81.6**		46.0	
Handle	First	90.0	(12.0)	35.0	(4.8)	69.4	(14.0)	22.8	(6.7)
	Last	51.4	(9.7)	18.5	(2.6)	43.4	(11.6)	22.9	(4.4)
	% decrease	42.9*		47.1*		37.5		-0.7	
Swallow	First	76.9	(7.6)	131.2	(11.4)	70.6	(8.8)	103.1	(13.6)
	Last	59.6	(5.1)	63.3	(5.8)	46.6	(4.8)	77.0	(10.0)
	% decrease	22.5		51.7**		34.1*		25.4	
Total time	First	532.1	(93.8)	500.6	(68.0)	499.5	(80.9)	553.6	(151.1)
	Last	155.2	(16.5)	132.9	(11.7)	156.1	(16.5)	331.0	(74.7)
	% decrease	70.8**		73.5**		68.8**		40.2	

Note. F = fish diet; W = worm diet; FW-F = mixed diet when feeding on fish; FW-W = mixed diet when feeding on worms; % decrease = % decrease in duration between first and last tests, obtained by subtracting the latency of each phase at the second test from the first and then dividing by the latency of the first test; total time = capture to swallow time.

^aApproach latencies and handling times for this group increased slightly.
* $p < .01$. ** $p < .001$.

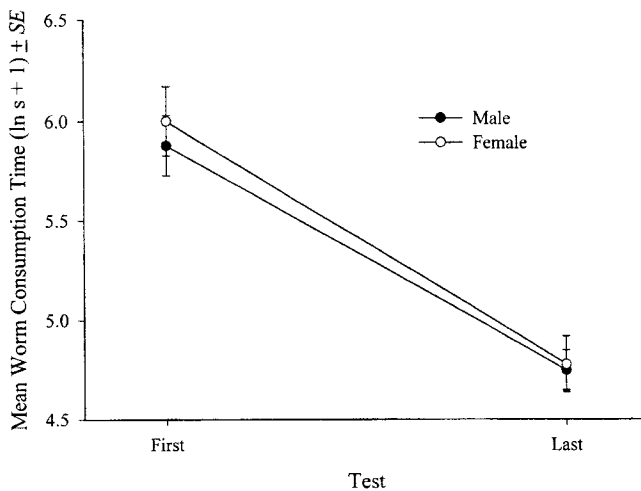
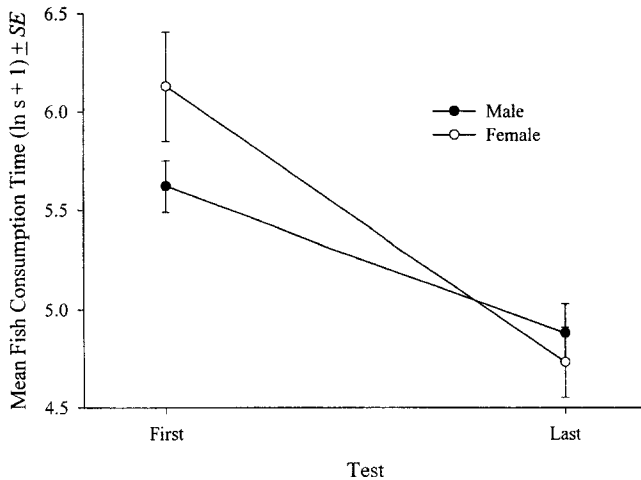


Figure 3. (Top panel) Sex differences in consumption times on the first and last tests for the fish-fed garter snakes. (Bottom panel) Sex differences in consumption times on the first and last tests for the worm-fed garter snakes.

$t(41) = 6.58, p = .0001$; and the FW group, $t(19) = 4.11, p = .001$, when feeding on fish. Capture times decreased the least for the FW group when tested on worms, and the change was not significant, $t(19) = 1.58, p = .131$. For the F and W groups, there were no significant sex, litter, or interaction effects.

The snakes in all three diet groups showed some evidence of changes in preference for particular prey body regions when seizing prey. Snakes in the F group captured fish at the head (first test, $n = 13$; last test, $n = 12$), the midbody (first test, $n = 17$; last test, $n = 21$), or the tail (first test, $n = 10$; last test, $n = 7$). Midbody captures were more likely than tail or head captures on both tests, which was statistically evident on the last test, $\chi^2(2, N = 40) = 7.55, p = .023$. Snakes in the W group showed a significant change from predominantly end (first test, $n = 27$; last test, $n = 17$) to midbody (first test, $n = 15$; last test, $n = 25$) captures, Cochran's $Q(1, N = 42) = 4.55, p = .033$. No attempt was made to distinguish if the head or the tail was seized.

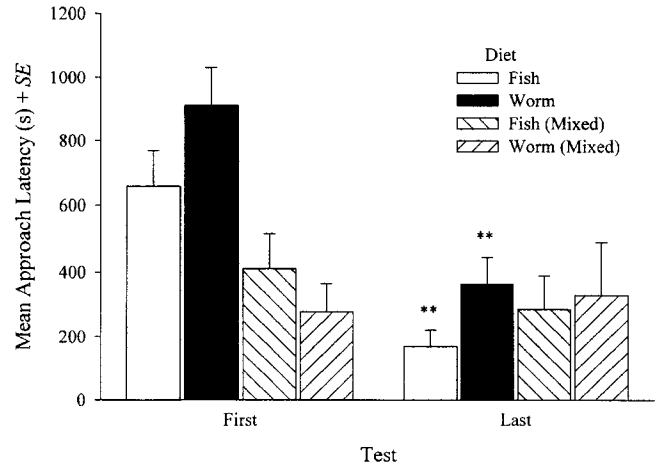


Figure 4. Mean (+SE) total approach latencies for the garter snakes in the three diet groups on the first and last tests. $**p < .0001$ represents significant decreases in approach latencies between the first and last tests.

Snakes in the FW group also seized fish by the head (first test, $n = 5$; last test, $n = 7$), the midbody (first test, $n = 12$; last test, $n = 8$), or the tail (first test, $n = 3$; last test, $n = 5$). Midbody captures by snakes in the FW group were significantly more likely on the first test with fish, $\chi^2(2, N = 42) = 6.70, p = .035$, but there was no significant difference on the last test. Worms were also captured by the end (first test, $n = 12$; last test, $n = 6$), or the midbody (first test, $n = 8$; last test, $n = 14$), and these changes were not significant at the .05 level, Cochran's $Q(1, N = 20) = 3.60, p = .058$.

Prey handling. Changes in prey handling times did not significantly differ among the groups, $F(3, 118) = 1.40, p = .245$. However, the F group showed an increased efficiency in prey handling beyond that of the other groups. The FW group did not show the same degree of improved fish

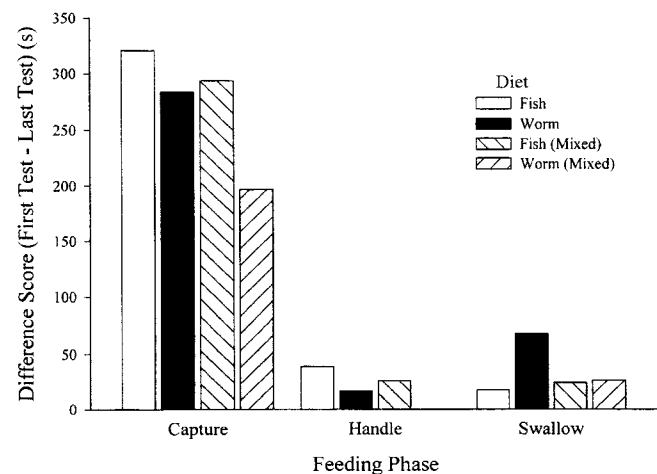


Figure 5. Mean difference scores for the garter snakes in the three diet groups for capturing, handling, and swallowing prey. The mean difference score in handling time for the worm (mixed) group was -0.66 s.

handling efficiency but nonetheless showed a slightly greater improvement than did the W group that was fed worms exclusively. The FW group showed less improvement in worm handling ability compared with the W group (see Figure 5 and Table 2). Only snakes feeding on single prey items showed significant decreases in handling times between the first and last tests: for the F group, $t(39) = 2.23$, $p = .028$, and for the W group, $t(41) = 2.20$, $p = .033$ (see Table 2), although snakes in the FW group showed a marginally significant decrease in fish handling time, $t(19) = 1.99$, $p = .061$. There were no significant sex effects, but for the F and W groups, there were significant litter effects for handling times on the first test, $F(17, 58) = 2.64$, $p = .016$, as well as the last test, $F(17, 58) = 2.64$, $p = .016$. Significant diet effects on handling times were also found for the first test, $F(1, 58) = 13.01$, $p = .001$, and the last test, $F(1, 58) = 16.42$, $p = .001$.

We expected that snakes would drop their prey more during the first test than the last test. However, rates of prey dropping were quite low throughout both tests, and no significant differences between tests were found within each diet group. The W group did not show a significant reduction in prey drops between the two tests, although drops on the last test were less likely (8 drops on the first test vs. 2 drops on the last test, $p = .109$). The greater incidence of drops by the worm-fed snakes during the first test may have been a reaction to body mucus, because head rubbing frequently followed prey drops (see D. S. Cunningham & Burghardt, in press). However, the relative amounts of prey consumed by the snakes appeared to influence prey dropping. The FW group was more likely than the F group to drop fish on the last test ($U = 310.0$, $p = .042$), whereas the FW group did not drop worms more than the W group ($U = 400.0$, $p = .325$).

Prey swallowing. The degree to which swallowing times decreased among the groups differed significantly, $F(1, 118) = 2.79$, $p = .044$. Figure 5 shows the differences in swallowing times for the three groups. Post hoc comparisons revealed a significant decrease ($p = .035$) in swallowing time in the W group ($M = 67.9$ s, $SE = 11.7$ s) compared with the F group ($M = 17.3$ s, $SE = 9.1$ s). The W group showed a significant decrease in swallowing times between the first and last tests, $t(41) = 5.93$, $p = .0001$, as did the FW group when feeding on fish, $t(19) = 2.42$, $p = .026$ (see Table 2). The F and FW groups decreased their swallowing times, although not significantly so: for the F group, $t(39) = 1.96$, $p = .057$; for the FW group, $t(19) = 1.78$, $p = .091$. There were no significant effects of litter on swallowing times for either test, but sex had a significant effect on swallowing time for the last test, $F(1, 58) = 6.09$, $p = .021$. A significant effect of diet on swallowing time was found for the first test, $F(1, 58) = 19.12$, $p = .001$, but was absent for the last test.

Worms were typically swallowed from the capture location. Fish were swallowed only from the head or the tail. Thus, fish that were captured from the midbody were always maneuvered to either the head or the tail before the onset of swallowing. Head-first swallowing was most common in the F group (first test, $n = 23$; last test, $n = 25$), but its

prevalence was not statistically significant over tail-first swallowing (first test, $n = 17$; last test, $n = 15$) at either test, Cochran's $Q(1, N = 40) = 0.18$, $p = .670$. The W group was more likely to swallow worms from either end on the first test (end first, $n = 30$; midbody first, $n = 12$) and showed no bias on the last test (end first, $n = 21$; midbody first, $n = 21$). This resulted in a significant reversal from a biased to an unbiased capture location, Cochran's $Q(1, N = 42) = 4.26$, $p = .039$. The FW group showed no bias for swallowing direction for fish on either the first or the last test (for both tests, head first, $n = 13$; tail first, $n = 7$). However, similar to the W group, the FW group was more likely to swallow worms from the end on the first test (end first, $n = 16$; midbody first, $n = 4$) and showed a reduction in this bias on the last test (end first, $n = 8$; midbody first, $n = 12$), Cochran's $Q(1, N = 20) = 6.40$, $p = .011$.

Discussion

The predatory abilities of *Thamnophis sirtalis* improved with experience, but diet influenced the degree to which this improvement occurred. Fish consumption times decreased regardless of whether snakes were fed exclusively fish or both fish and worms. Worm consumption times also decreased with experience, but the improvement was significantly greater if fish were not eaten as well. A similar result was called an "interference" effect by Yeager, Burghardt, and Lyman-Henley (1996), in which snakes that switched prey types after experience with one type of prey showed a decrement in consumption ability with novel prey.

The relative improvements of some consumption phases are prey-dependent. Unlike snakes reared on a single prey type, those reared on a mixed diet showed no significant decreases in approach latencies between the two tests. Thus, feeding on a mixed diet may interfere with prey detection and assessment. However, on the first test the approach latencies of the FW group were already much shorter than those of the F and W groups, although this difference was significant only for worms. Total consumption times (excluding approach) among all groups were similar for the first tests. The significant reduction in approach times to worms in the FW group compared with the W group was most likely due to a carryover effect from the prior test with fish.

The snakes in the W group showed a greater decrease in swallowing times between the two tests than the snakes in the FW group when tested on worms. Worm swallowing times may have been suppressed because of feeding on a mixed diet. However, the FW group consumed only half of the total number of worms consumed by the W group. Thus, they had less experience with swallowing worms between the two tests. If this is true, then this relative lack of experience did not affect responses to swallowing fish in the FW group.

Overall, the snakes did not drop prey more often on the first test than on the last test, but the FW group dropped fish more than the F group on the last test, suggesting an interference effect and thus a cost for being on the mixed diet. Snakes in the F and FW groups showed no biases toward swallowing fish from either the head or the tail. In

contrast, snakes in the W and FW groups were more likely to swallow worms end-first on the first test but showed no bias on the last test. This result is probably due to the fact that worms were predominantly captured from the end first on the first test, whereas midbody captures were more frequent on the last test. Snakes typically swallowed worms from the same regions in which the prey were seized. Because of morphological differences, worms require less actual maneuvering before the onset of swallowing. Regardless, none of the groups differed in the degrees to which handling times decreased.

Litter and Sex Differences

Unlike many studies of garter snakes (e.g., Brodie & Garland, 1993), differences due to litter were mostly nonsignificant in the present study. This could be due to the restricted population from which the mothers of the tested snakes were derived. However, the litters were small and divided into three feeding groups. Given the Sex \times Diet \times Litter interaction found at the first test, the minimal family (genetic) variation may not be surprising. The presence of litter effects on prey consumption and its phases suggests that further work is needed for exploring potentially heritable variation of these behaviors.

Sex differences were found for snakes in the F group. Males were able to consume fish more rapidly than females at their first feeding, but females showed a greater overall decrease in fish consumption time at the last test. That this effect was not due to a motivational difference is suggested by the fact that worm consumption times were virtually identical for the two sexes at both feedings. This unexpected result warrants further exploration. In some populations of *Thamnophis sirtalis*, larger snakes shift to fish and amphibian diets (Fitch, 1999), and females grow larger than males, often reaching a weight more than twice that of males. Females may thus have evolved a greater suite of adaptations for learning to deal with diverse prey than have males. Wild *Thamnophis sirtalis* shift to fish diets when available, such as at fish hatcheries (Gregory & Nelson, 1991). The sex difference in diet in natural populations is typically interpreted as size-related resource partitioning between the sexes or possibly as due to sex-related differences in relative head-to-body sizes. Female *Thamnophis sirtalis* have been shown to have greater relative head sizes than males (Shine & Crews, 1988), which may allow for increased fish handling abilities and probability of consumption. The presence of sexual size dimorphism in head size has been reported for neonatal brown snakes (*Storeria dekayi*; King, 1997). Further explorations on the development of head-size dimorphism in *Thamnophis sirtalis*, and whether head size affects feeding abilities, are needed.

Local Adaptation and Population-Typical Diets

Unlike prior studies of *Thamnophis sirtalis* (e.g., Scudder-Davis & Burghardt, 1987), in the present study snakes that fed exclusively on fish grew less than those that fed exclusively on worms. This may be a consequence of this population being adapted to a primarily earthworm diet. It is

unlikely that growth rates were biased by rejection of either prey type because feeding records indicated nearly equal proportions of prey consumed by each group. Lyman-Henley and Burghardt (1995) found that growth rates of *Thamnophis butleri*, an earthworm specialist, that were fed worms exceeded those of *Thamnophis butleri* reared on fish. Perhaps this result can be explained by locally adaptive, physiological responses for worm digestion and assimilation, but further exploration of this result is needed.

Plasticity and Feeding Strategies

Experience plays an important role in the development of foraging ability in various generalist snake species (e.g., Burghardt, 1978; Drummond, 1983; Halloy & Burghardt, 1990; Mori, 1996; Yeager, Burghardt, & Lyman-Henley, 1996). The same also applies to generalist species belonging to different taxa, such as bluegill sunfish (*Lepomis macrochirus*; Ehlinger, 1989), 15-spined sticklebacks (*Spinichia spinachia*; Croy & Hughes, 1991b), and shorecrabs (*Carcinus maenas*; P. N. Cunningham & Hughes, 1984).

Increased foraging efficiency may benefit organisms in a variety of ways, such as by reducing energy expenditure or decreasing predation risks. Importantly, the lack of dietary specializations may impose some constraints on generalist species such as *T. sirtalis*. These constraints can be alleviated if a species is capable of increasing foraging efficiency with experience on different prey, which *T. sirtalis* is capable of doing. Generalist species such as *T. sirtalis* successfully invade new habitats and feeding niches, which apparently occurs at any age (Gregory & Nelson, 1991). Therefore, selection could act to maintain the capacity for improvements in foraging abilities through adulthood. Prey specialist species, such as *Thamnophis melanogaster*, also show improvements in prey handling with experience, but this ability may diminish after early experience with the prey on which they specialize. Thus, another potential difference between prey generalist and specialist species may lie in the greater retention of learning capacities throughout ontogeny in the former. Prey size selection may also be an important difference between neonatal, juvenile, and adult animals (Arnold, 1993; Yoerg, 1994). Snakes that often undergo size-dependent shifts in prey species, such as *Thamnophis sirtalis* (Fitch, 1965), may also be more likely to improve in foraging skill when these developmental shifts take place. An important question is whether a generalist species, such as *Thamnophis sirtalis*, reared entirely on one food (e.g., earthworms) is more plastic as an adult than a specialist earthworm-eating snake such as *Thamnophis butleri*.

Individual variability in the development of foraging efficiency was documented in this study. The implications this finding has for natural situations are in need of closer examination. Werner, Mittelbach, and Hall (1981) found that superior learning abilities facilitate changes in food habitat specializations. Individuals that are capable of incorporating information more rapidly than others may be more capable of invading novel feeding niches, or of switching to more profitable ones (Gotceitas & Colgan, 1988). Even within a given habitat, learning ability may also serve as a good predictor of diet. With regard to snakes, those that are

capable of rapidly acquiring prey detection and handling skills may have an advantage over slower learners. This could result in partitioning of food resources on the basis of learning abilities. Thus, in addition to the genetic differences that underlie microevolutionary changes in prey detection and handling in snakes (Drummond & Burghardt, 1983), learning capabilities may also influence prey choices within populations; explain observed differences among them; and interact with diet, growth, sex, morphology, and reproductive fitness (Burghardt, Layne, & Konigsberg, in press).

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Received November 6, 1998

Revision received February 19, 1999

Accepted February 23, 1999 ■