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NEONATAL PLASTICITY AND ADULT FORAGING BEHAVIOR IN GARTER SNAKES (*THAMNOPHIS SIRTALIS*) FROM TWO NEARBY, BUT ECOLOGICALLY DISSIMILAR, HABITATS

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ABSTRACT: The widely distributed Common Gartersnake (*Thamnophis sirtalis*) thrives in a variety of environments and preys upon a diversity of species. Phenotypic plasticity (including learning), as well as genetic diversity, may underlie the success of this species. We examined how different types of feeding experience influence the ontogeny of foraging behavior in garter snakes from two populations with different adult diets (earthworm or amphibian/worm/mammal diets) living on Beaver Island in Lake Michigan. Times to approach, capture, handle, and swallow prey were recorded in controlled laboratory settings. In Experiment I, neonatal snakes reared on fish, earthworms, or a mixed diet were tested for feeding skills at their first feeding, and at 5 subsequent intervals after feeding experience and diet-switching over a period of nearly 8 months. Snakes in all three groups decreased their latencies to consume prey after feeding experience and there were some litter, but no site or sex, differences. Snakes fed initially on worms were slow at consuming fish upon diet switching, whereas snakes that initially fed on fish rapidly consumed worms upon their first feeding. Feeding skills for initial prey were retained following the diet-switching phase. Experiment II determined the effects of long-term feeding experience on the abilities of field-caught adult snakes to detect, capture, and consume frogs, fish, and worms. Most foraging measures differed for all three prey, but there were few site differences and no sex differences. The effects of prior feeding experience appear to be less evident for adults than for neonates, which may be due to the effects of changing predator-prey body size relationships, changes in prey availability, or to constraints of the captive testing environment. Although populations on the island eat different prey, there is little evidence for genetic differentiation in foraging behavior during the several thousand years that the island has existed.

Key words: *Thamnophis*; Garter snake; Plasticity; Foraging

THE TYPES OF environments in which animals forage, and the variability of prey abundance across both spatial and temporal scales, are known to influence the degree to which foraging efficiency increases with feeding experience (Day and McPhail, 1996; Ehlinger, 1989; Krebs and Inman, 1994). The Common Gartersnake (*Thamnophis sirtalis*), the most geographically widespread species of snake in North America, feeds on a diversity of prey species that vary in spatial and temporal abundance (see Rossman et al., 1996). The progeny of predatory and habitat generalists, such as neonatal *T. sirtalis*, may be born into highly fluctuating environments where learning is vital to foraging success; their survival may depend upon their abilities to detect, capture, and consume prey. Empirical studies have demonstrated a

close relationship between juvenile survival, reproductive success, and foraging proficiency (Sih, 1993). For example, birds that are slow to acquire foraging skills are known to delay breeding, starve, or suffer increased predation risk (see Yoerg, 1994). Even highly precocial species may require feeding experience in order to forage efficiently (Burghardt and Krause, 1999; Croy and Hughes, 1991a,b; Day and McPhail, 1996; Mori, 1996; Savitsky and Burghardt, 2000).

One way to deal with diverse habitat and prey resources is to genetically adapt to different settings. In a widespread species, such as *Thamnophis sirtalis*, such local adaptation is both possible and demonstrated (Burghardt and Schwartz, 1999). Studies on neonatal snakes have shown heritable differences at birth in several species (reviews by Burghardt, 1993; Brodie and Garland, 1993). In fact, within litters, neonatal garter snakes can strongly

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prefer fish or earthworms, and this could be a maternal 'bet hedging' strategy (Burghardt, 1975). However, gene flow may be considerable in contiguous populations and thus counter selection for between population differences. Thus, phenotypic plasticity, not genetic adaptation, may be more likely to occur in such situations. Even prey specialist snakes such as the water snake, *Nerodia rhombifer*, may develop proficiency over the first months of life (Savitsky and Burghardt, 2000).

Nevertheless, although plasticity, especially learning, may be beneficial, there are costs to relying on experience for developing foraging skills. These include increases in both predation risk and time and energy devoted to finding and consuming prey. These costs may be most evident during early development, and have been reported in studies comparing specialist and generalist snake species. For example, neonates of generalist species are often inferior in foraging proficiency compared to morphologically and behaviorally specialized snakes (e.g., Drummond, 1983; Halloy and Burghardt, 1990; Mori, 1994, 1996). However, with experience predatory generalists can become nearly as proficient at consuming prey as specialist species. For example, Mori (1996) compared rodent handling in hatchling, yearling, and juvenile *Elaphe climacophora*, a rodent specialist, with *E. quadrivirgata*, a dietary generalist. After feeding experience, *E. quadrivirgata* were nearly equal in rodent handling ability to *E. climacophora*, whereas younger snakes were much less adept than *E. climacophora* at handling rodents.

Efficiently detecting, capturing, and consuming prey may minimize predation risks for garter snakes that forage in open fields, along water banks, and under water, where they themselves may be highly vulnerable to predators. The foraging repertoire of *Thamnophis sirtalis* shows a high degree of plasticity (Burghardt, 1993; Burghardt and Krause, 1999; Halloy and Burghardt, 1990). *T. sirtalis* is capable of detecting, subduing, and consuming a wide variety of prey species including annelids, fish, amphibians, mammals and birds. The

rapid acquisition of feeding skills by *T. sirtalis* would aid in reducing the costs of being relatively unspecialized. Behavioral plasticity would facilitate the acquisition of feeding on both novel and species-typical prey. For example, *T. sirtalis* in most populations feed on earthworms and a variety of amphibian species, but will feed on fish opportunistically in the field and readily in captivity (Arnold, 1992; Carpenter, 1952; Gregory and Nelson, 1991; Nelson and Gregory, 2000). However, neonatal *T. sirtalis* are not very adept at handling fish in comparison to *Thamnophis melanogaster*, an aquatic prey specialist (Halloy and Burghardt, 1990). With feeding experience, *T. sirtalis* is capable of consuming fish about as proficiently as *T. melanogaster*, thus benefiting from behavioral plasticity.

The degree to which learning contributes to the development of feeding skills may be condition dependent. That is, diet may determine how efficiently an individual will be in detecting, capturing, handling, and swallowing prey. For example, feeding on a mixed prey diet may impede predator learning (Burghardt and Krause, 1999; Cunningham and Hughes, 1984). Thus, there are potential costs to feeding on a mixture of prey species. The costs, however, may not outweigh the benefits of feeding on several prey species. Furthermore, feeding on one type of prey may facilitate switching to another type, but interference effects can impede a predator's ability to undergo dietary shifts (Yeager et al., 1996). Interference effects can occur when a predator switches from a relatively easy prey to feed on, to a more difficult one. Retaining feeding skills may be critical as well, as costs may accrue if an individual forgets how to locate, capture, and consume prey (Hughes and Blight, 1999; Krebs and Inman, 1994; Shettleworth, 1998).

Previously, we tested three groups of neonatal *T. sirtalis* on their abilities to feed on fish, worms, or a mixed diet (Burghardt and Krause, 1999). Initially, all prey items took equally long to consume. However, after the three diet groups had 11 to 12 feedings on their respective diets, fish consumption times decreased significantly,

and worm consumption times decreased for snakes feeding exclusively on worms. Also, the phases of predation were differentially affected by feeding experience. Fish and worm detection, as measured by prey approach times, decreased significantly after feeding experience by snakes reared on pure diets, but not for snakes reared on mixed diets. Feeding on a mixed diet also appeared to interfere with the development of approaching, capturing, handling, and swallowing worms. The present study extends this work in several directions by 1) including animals from two different, but nearby, sites where the animals live in different habitats and forage for different prey, and 2) observing foraging by adults freshly captured from each site.

The snakes in the Burghardt and Krause (1999) study originated from pregnant females captured on McCafferty farm on Beaver Island (Charlevoix County, MI). Beaver Island is the largest island in Lake Michigan and is part of an archipelago located in the north region of the lake 18 miles from the lower Michigan peninsula. The island emerged after the last glacial period, roughly 9000 years ago and measures 21 km long and 10.5 km wide. Much of the work done on Beaver Island *T. sirtalis* has taken place at or near McCafferty farm (Burghardt and Krause, 1999; Burghardt et al., 2000; Gillingham et al., 1990; Krause, 2000), where the snakes primarily feed on earthworms. The present study compares snakes from two sites, Miller's marsh and McCafferty farm, separated by a relatively short distance (10 km). Miller's marsh hosts a much wider variety of prey items, including several species of amphibians, as well as earthworms. Prior research at or near these two sites has consistently revealed amphibian and worm stomach contents in the snakes from Miller's marsh, and only earthworms in the snakes from McCafferty farm (Dickinson, 1979; Gillingham and Burghardt, unpublished; Krause, 2000).

The findings reported in Burghardt and Krause (1999) lead to further questions about the ontogeny and plasticity of neonatal garter snake foraging behavior. These questions were addressed in Experiment I

of this study. The first question concerns the age at which young snakes reach asymptotic levels of prey consumption efficiency. The second question concerns the effects of switching from difficult to relatively easy to consume prey, and the reverse. It appears that feeding on fish, a prey item that is relatively difficult to consume, may facilitate switching to worms, which are easier to consume. Conversely, feeding on worms may interfere with switching to fish (Yeager et al., 1996). Will feeding on a mixed diet confer any foraging efficiency advantage over snakes reared on a single diet? The third question concerns the ability of garter snakes to retain acquired foraging skills after a period of having to depend on other prey, as may occur when snakes are confronted with periodic and extended fluctuations in prey abundance. Thus, the retention of feeding skills by garter snakes needs to be assessed. Forgetting how to handle prey has been reported in sticklebacks, *Spinachia spinachia* (Croy and Hughes, 1991a; Mackney and Hughes, 1995) and this possibility was tested for garter snakes in Experiment I. A fourth question concerns whether snakes from the two populations with different food resources would either differ at birth in foraging proficiency on earthworms or fish, or in the plasticity of their learning.

The applicability of laboratory studies of neonatal garter snake foraging behavior (e.g., Burghardt and Krause, 1999; Halloy and Burghardt, 1990; Experiment I of this study) to natural situations was tested in Experiment II. Adults captured from the two ecologically dissimilar sites were tested on their abilities to prey upon fish, frogs, and worms. Based on the dietary differences between the two sites, adult garter snakes from McCafferty farm should have greater difficulty feeding upon large amphibians than snakes from Miller's marsh. Fish have not been recorded in the stomach samples from snakes at either site. We included fish prey in Experiment II to test whether snakes from Miller's marsh, owing to their more diverse diets, would show superior feeding skills on novel prey compared to snakes from Mc-

TABLE 1.—Experiment I prey feeding skills testing schedule for the three diet groups.

Feeding test (FT)	Age (days)	Diet group		
		Fish (F) test prey	Worm (W) test prey	Mixed (FW) test prey
FT1	20	Fish	Worm	Fish & Worm
FT2	98–103	Fish	Worm	Fish & Worm
FT3	178–183	Fish	Worm	Fish & Worm
FT4	181–186	Worm	Fish	—
FT5	226–231	Worm	Fish	—
FT6	229–232	Fish	Worm	—

Cafferty farm. Finally, we predicted equal worm consumption abilities by snakes from both sites.

EXPERIMENT I: DIETARY EFFECTS ON FEEDING SKILLS IN YOUNG GARTER SNAKES

In this experiment, we manipulated the diets and feeding schedules of young garter snakes such that the effects of initial feeding experience, prey switching, and retention of feeding skills could be assessed. One diet group was initially fed fish, and then had their diets switched to worms. A second diet group was initially fed worms, and had their diets switched to fish. Following the diet-switching phase, both groups were re-tested for feeding skills on their initial prey type. A third group was fed a mixed diet throughout the duration of the study to compare with the single diet groups. In addition to examining the ontogeny of feeding skills in these three groups, when possible we tested for the effects of sex, site, and litter on feeding behavior.

Although the adult diets of the snakes from McCafferty farm and Miller's marsh differ, neonatal diets are not known. It is assumed that most young garter snakes begin life feeding on earthworms and later shift to other prey (Carpenter, 1952; Fitch, 1965; Greenwell et al., 1984). However, to test whether snakes from the two sites differed at birth in either initial foraging ability, or ability to profit by feeding experience, we tested neonates born to mothers from both sites.

MATERIALS AND METHODS

Subjects were 106 neonatal garter snakes (54 males, 52 females) from 16 lit-

ters (mean litter size = 6.6, range = 1 to 15) born in the fall of 1998 to mothers collected at McCafferty farm ($n = 43$, 9 litters) and Miller's marsh ($n = 63$, 7 litters). Within 24 h of birth the snakes were sexed, weighed, measured and housed separately in clear plastic cages ($13.5 \times 18.5 \times 4.0$ cm), each including a cardboard substrate, shelter, and water dish. Room temperature was kept constant (25 C), with 30% relative humidity, and a 12:12-hr light:dark cycle was maintained throughout the study period. Cages were cleaned as needed and water was available *ad libitum*.

At birth, neonates were assigned to diets of either fathead minnows, *Pimephales promelas*, (F group, $n = 35$ snakes), leaf-worms, *Lumbricus rubellus*, (W group, $n = 41$ snakes), or a combination of the two (FW group, $n = 30$ snakes). These prey were chosen because they are abundantly available through commercial suppliers, and they match or are close matches to prey normally consumed by garter snakes. A split litter and sex design was used, with individuals from each litter, site, and sex randomly assigned as equally as possible across each diet group. At 14 and 17 days of age, prior to the feeding tests, all snakes were tested for chemosensory responses to brief exposures to fish and worm prey extracts.

The snakes were given six feeding tests (FT1–FT6). Table 1 summarizes the testing schedule for Experiment I. At 20 days of age, each snake was offered its first live prey (FT1). During each feeding test, the FW group was tested on both prey types, presented in random order, with three days separating the two trials. FT2 was

TABLE 2.—Dependent measures used for feeding test in Experiments I and II.

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 end of approach latency to when prey is seized in the snake's jaws.
Handling time	Number of seconds from prey seizure to when prey is maneuvered into place such that it can be swallowed.
Swallowing time	Number of seconds from time snake begins side to side jaw movements (jaw walking), which pushes prey into the throat, until first post-ingestion tongue flick.
Total consumption time	Number of seconds from onset of capture to first postingestion tongue flick.

completed 80–85 days after FT1, with the snakes receiving 11 or 12 weekly meals in between testing sessions. FT3 was completed after another 80–85 days, with the snakes still feeding on their initial diets during this interval. Following FT3, the diets of the F and W groups were reversed. FT4, representing the first time these snakes encountered a new prey item, was conducted on the F and W groups only, three days following FT3. FT5 was completed 45 days following FT4, with the snakes receiving 11 or 12 meals in between testing sessions. To meet increasing dietary needs, all snakes were fed twice weekly between FT4 and FT5. To assess the snakes' retention for the original dietary experience, prey items were then reversed again back to the original diet at FT6. FT6 was completed within 3 days after FT5.

Live prey items weighing 10–15% of each snake's body weight were placed in petri dishes in the center of each snake's home cage for each one-hour test. Water and a shallow layer of dirt were placed in each dish for fish and worms, respectively. Tests were either videotaped with a Hi-8 camcorder (Sony CRD-VX3) or recorded on check sheets through live observation. Table 2 describes the dependent measures recorded at each test. In addition to these measures, descriptive measures including prey capture locations, prey orientation during swallowing, and the number of times prey were dropped were recorded. Prey items were removed if snakes had not eaten by the end of each one-hour test, and additional tests of the same prey spe-

cies were run every second or third day until the snakes ate.

Statistical Tests

Effects of sex, litter, and site on total consumption time and each feeding phase were tested at FT1 using a MANOVA. Sex and site were specified as fixed factors, with litter treated as a random factor nested in site. Wilk's Lambda (λ) was used to test for multivariate effects of each of the three factors. Separate univariate *F*-tests were used to examine the effects of sex, site, and litter on each feeding phase and total consumption times.

Changes in overall consumption times between FT1, FT2, and FT3 were tested using repeated measures ANOVA. The F and W groups were compared with diet treated as the grouping variable, and the interaction testing for relationships between diet and test (FT1–FT3). Changes in latencies to complete each feeding phase at FT1, FT2, and FT3 were tested using repeated measures ANOVA. The FW group was also tested with repeated measures ANOVA, comparing FT1–FT3 for its consumption times and latencies to complete each feeding phase on fish and worm, separately. The effects of diet switching (FT4 and FT5) on total consumption times and feeding phases were evaluated using Wilcoxon signed-ranks tests for the F and W groups separately. The final feeding test, FT6, was compared with FT3 using Wilcoxon signed-ranks tests to evaluate whether prey consumption times, or the phases comprising it, increased following diet reversals for the F

TABLE 3.—Results of *F*-tests for Litter, Site, and Sex effects on each prey consumption phase and total consumption times by neonatal garter snakes at their first feedings (FT1). Significant *P*-values are boldfaced.

Source	DV	df	Hypothesis MS	Error MS	<i>F</i>	<i>P</i>
Litter Within Site	Approach	14, 78	1.94	1.78	1.09	0.377
	Capture	14, 78	4.75	2.55	1.86	0.044
	Handle	14, 78	1.34	1.16	1.16	0.325
	Swallow	14, 78	0.35	0.22	1.57	0.107
	Total	14, 78	2.20	1.21	1.82	0.051
Site	Approach	1, 14	6.64	1.94	3.42	0.086
	Capture	1, 14	0.05	4.75	0.01	0.923
	Handle	1, 14	0.00	1.34	0.00	0.922
	Swallow	1, 14	0.01	0.35	0.04	0.842
	Total	1, 14	0.09	2.20	0.04	0.844
Sex	Approach	1, 14	1.08	1.94	0.55	0.469
	Capture	1, 14	1.05	4.75	0.22	0.645
	Handle	1, 14	0.13	1.34	0.10	0.762
	Swallow	1, 14	0.10	0.35	0.28	0.602
	Total	1, 14	0.22	2.20	0.10	0.756

and W groups. The data analyzed with multivariate tests were normalized using natural log (+1) transformations.

RESULTS

Feeding records indicated that similar proportions of fish and worms were eaten by snakes in all diet groups. The snakes in the F group consumed 88.2% of fish offered (mean = 24.2). The W group consumed 88.6% (mean = 23.4) of worms. The FW group consumed 91.3% of fish (mean = 11.3) and 87.2% of worms (mean = 13.7). No significant changes were found in prey capture location or swallowing direction, or the number of times prey were dropped between testing sessions, and these measures were dropped from further analyses. The results presented below first cover litter, sex, and site effects on each feeding phase and total consumption times, followed by analyses of overall changes in prey consumption times and phases between FT1 and FT3, and the effects of diet on these changes. Following are results on diet switching (FT4 and FT5) and tests for retention of feeding skills (FT3 and FT6).

Litter, Sex, and Site Effects

At FT1, there were no overall effects for litter ($\lambda = 0.35$, $F_{5,10} = 1.24$, $P = 0.10$), site ($\lambda = 0.76$, $F_{5,10} = 0.65$, $P = 0.668$), or

sex ($\lambda = 0.94$, $F_{5,10} = 0.13$, $P = 0.982$). Univariate *F*-tests revealed marginal litter effects ($P < 0.05$) for capture time and total consumption time at FT1 (Table 3). All interactions between litter, site, and sex were not significant. A second MANOVA was run to determine whether the neonates from Miller's marsh and McCafferty farm differed in their abilities to consume fish or worms at their first feeding. Site and prey type (diet) were treated as fixed factors and litter was treated as a random factor nested within site. The interaction between site and diet was included to test for geographic variation in fish or worm feeding skills. The results from this MANOVA revealed a non-significant interaction between site and diet ($\lambda = 0.94$, $F_{5,74} = 0.99$, $P = 0.430$). No significant results were found for litter, sex, or site at FT2 or FT3. Therefore, data for these three factors were pooled for all subsequent tests.

Initial Feeding Experience

Total consumption times.—Predatory experience played a significant role in the development of the snakes' feeding skills. The snakes in all three diet-groups showed improvements in overall prey consumption abilities following feeding experience (see Figure 1). Table 4 summarizes the results for total consumption times and each feeding phase for the

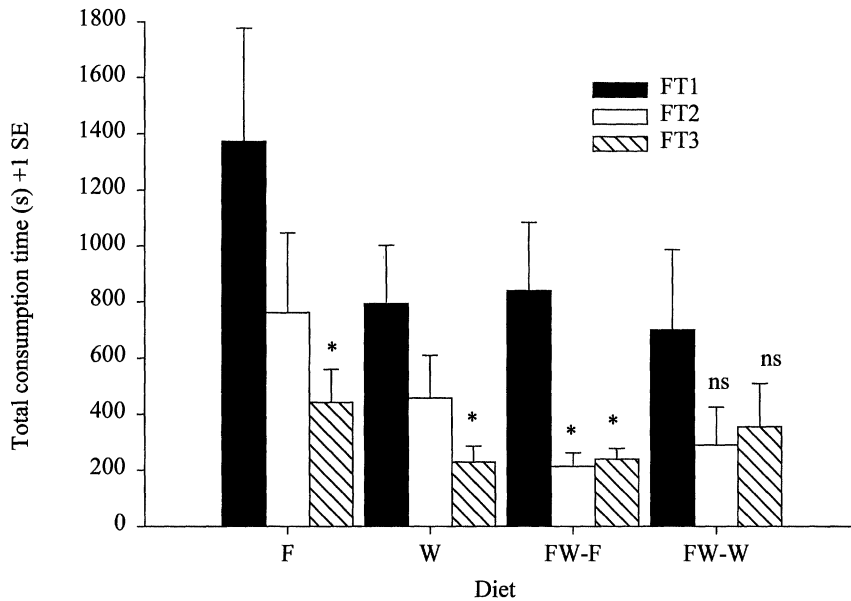


FIG. 1.—Mean (+1 SE) total consumption times for garter snakes in each diet group at FT1, FT2, and FT3. F = Fish group, W = Worm group, FW-F = Mixed group (fish), FW-W = Mixed group (worm). * = $P < 0.05$ significant decrease in mean consumption time between FT1 compared with FT2 and FT3.

three diet groups at FT1 through FT3. The summary statistics in Table 4 include only those snakes that ate at each test period. The snakes in the F and W groups significantly decreased their prey consumption times between the three tests (Table 5). The F group reduced their fish consumption times by 44.5% between FT1 and FT2, and by 67.9% between FT1 and FT3. The W group reduced worm consumption times by 42.5% between FT1 and FT2, and by 71.3% between FT1 and FT3 (Table 4). The degrees to which consumption times decreased were the same between the F and W groups, as shown by a non-significant interaction between test and diet (Table 5). Total consumption times decreased between FT1 and FT2, but the difference did not reach significance ($P = 0.09$). A significant decrease in total consumption time was found between FT1 and FT3 ($P = 0.003$), and not between FT2 and FT3 ($P = 0.967$). The latter comparison (between FT2 and FT3) indicates that prey were consumed as rapidly as possible by 103 days of age.

Snakes in the FW group also decreased

their prey consumption times with feeding experience, but prey type affected the degree to which this occurred (Table 4). The FW group consumed fish more rapidly after feeding experience, and the change was significant (see Table 5). Pairwise comparisons revealed significant reductions in fish consumption times between FT1 and FT2 (74.7%, $P = 0.01$), and between FT1 and FT3 (71.7%, $P = 0.033$). Fish consumption times between FT2 and FT3 were not significantly different ($P = 1.0$). Worm consumption times for the FW-W group did not decrease significantly overall (see Table 5), or between any of the three tests. However, worm consumption times by the FW-W group were relatively rapid at their initial feeding (see Figure 1).

To determine whether changes in total consumption times differed among the three diet groups, difference scores were calculated by subtracting the total seconds of FT2 from FT1. A one-way ANOVA on these scores did not reveal a significant diet effect ($F_{3,65} = 0.31$, $P = 0.816$). Difference scores comparing FT1 and FT3

TABLE 4.—Mean (± 1 SE) latencies for each consumption phase at FT1, FT2, and FT3 for snakes completing each test in each diet group.

Phase	Test	Diet			
		F (n = 10)	W (n = 15)	FW-F (n = 9)	FW-W (n = 11)
		Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
		% diff	% diff	% diff	% diff
<i>Approach</i>	FT1	822.2 (313.62)	534.7 (125.89)	530.8 (230.97)	1292.5 (338.03)
	FT2	336.9 (115.70)	531.8 (181.58)	137.4 (47.52)	883.2 (365.28)
	FT3	301.7 (99.12)	484.2 (145.65)	309.9 (150.59)	282.0 (96.82)
<i>Capture</i>	FT1	1265.8 (414.79)	671.3 (206.63)	737.9 (250.53)	601.0 (288.73)
	FT2	594.9 (278.84)	386.1 (147.79)	73.0 (48.80)	218.8 (135.55)
	FT3	271.3 (92.82)	136.7 (52.20)	42.3 (8.14)	277.3 (153.97)
<i>Handle</i>	FT1	44.0 (27.61)	31.2 (6.28)	34.6 (12.07)	40.6 (15.66)
	FT2	36.6 (13.51)	17.7 (4.59)	75.4 (17.59)	26.6 (6.07)
	FT3	71.4 (34.11)	27.8 (8.31)	105.7 (27.71)	22.9 (13.06)
<i>Swallow</i>	FT1	61.9 (9.71)	90.9 (12.95)	66.8 (9.52)	57.2 (7.88)
	FT2	75.5 (16.03)	52.1 (8.01)	63.8 (14.76)	42.5 (6.91)
	FT3	97.8 (20.68)	63.2 (9.49)	89.9 (8.71)	52.3 (12.49)
<i>Total</i>	FT1	1371.7 (405.34)	793.4 (209.54)	839.2 (245.46)	698.8 (289.01)
	FT2	761.0 (285.28)	455.9 (152.82)	212.2 (48.54)	287.9 (134.59)
	FT3	440.5 (118.21)	227.7 (56.72)	237.9 (28.75)	352.4 (154.12)

Note: F = Fish group, W = Worm group, FW-F = Mixed group (fish), FW-W = Mixed group (worms). % diff. = decrease ("−") or increase ("++") between FT1 and FT2, and FT1 and FT3, * = $P < 0.05$, ** = $P < 0.001$ significant decrease between FT1 compared with FT2 and FT3.

TABLE 5.—Results from repeated measures ANOVAs testing for significant changes in total prey consumption times between the three test periods (FT1–FT3) by snakes in the Fish (F), Worm (W), and Mixed (FW-F, FW-W) diet groups.

Diet group tested	Source	df	MS	F	P
*F & W groups	Test	2	4.25	6.42	0.003
	Test × Diet	2	3.71E-02	0.03	0.968
	Error	46	1.13		
**FW-F	Test	2	3.42	10.66	0.001
	Error	16	0.32		
**FW-W	Test	2	2.28	1.62	0.223
	Error	20	1.41		

* The F and W groups were grouped as Diet, with the Test × Diet interaction testing for differences in the relative decreases in total prey consumption times between diet groups.

** Separate repeated measures ANOVAs were run for the Mixed (FW) diet group's total consumption times of fish (FW-F) and worms (FW-W). No interaction is tested because the snakes comprise a single (FW) diet group.

revealed similar results ($F_{3,43} = 0.33$, $P = 0.802$).

Comparisons by Feeding Phase

Approach latencies.—Results from repeated measures ANOVAs testing for the effects of feeding experience on changes in prey approach latencies are summarized in Table 6. Mean approach latencies to

prey by the F and W groups decreased between FT1 and FT2 and between FT1 and FT3 (Table 4), but the changes were not significant (Table 6).

Snakes in the FW group approached fish more rapidly between FT1 and FT2, and between FT1 and FT3. Approach latencies to worms by the FW group also decreased between FT1 and FT2, and

TABLE 6.—Results of repeated measures of ANOVAs testing for significant changes in approach latencies, and capturing, handling, and swallowing times between the first three test periods by snakes in the Fish (F), Worm (W), and Mixed (FW-F, FW-W) diet groups.

Feeding phase	Diet group tested	Source	df	MS	F	P
<i>Approach</i>	F & W groups	Test	2	1.47	0.99	0.379
		Test × Diet	2	0.38	0.26	0.775
		Error	46	1.48		
	FW-F	Test	1	4.46	2.54	0.110
		Error	16	1.76		
		Error	2	7.05	2.42	0.114
FW-W	Test	20	2.91			
	Error	2	18.59	7.42	0.002	
	Error	2	0.59	0.24	0.791	
<i>Capture</i>	F & W groups	Test	46	2.51		
		Test	2	18.97	16.39	< 0.001
		Error	16	1.16		
	FW-F	Test	2	4.30	1.49	0.250
		Error	20	2.89		
		Error	2	2.15	1.92	0.158
<i>Handle</i>	F & W groups	Test	2	1.30	1.16	0.322
		Test × Diet	2	1.12		
		Error	46	1.12		
	FW-F	Test	2	2.42	2.85	0.087
		Error	16	0.85		
		Error	2	1.78	1.38	0.274
<i>Swallow</i>	F & W groups	Test	20	1.28		
		Test	2	5.91E-02	0.20	0.823
		Test × Diet	2	1.56	5.16	0.009
	FW-F	Error	46	0.30		
		Test	2	0.56	3.18	0.069
		Error	16	0.17		
FW-W	Test	2	0.27	1.14	0.340	
	Error	20	0.23			

FT1 and FT3, but the changes were not significant overall for either diet group (see Tables 4 and 6). Pairwise comparisons among the three tests did not reveal any significant differences. The three diet groups did not significantly differ from each another in approach times at FT2 ($F_{3,41} = 1.24$, $P = 0.307$), or FT3 ($F_{3,41} = 0.82$, $P = 0.491$).

Prey capture.—Snakes feeding on single diets significantly reduced their prey capture times across the first three feeding tests (Table 6). Fish were captured more rapidly between FT1 and FT2 (53.0%), and between FT1 and FT3 (78.6%). Worm capture times decreased by 42.5% between FT1 and FT2, and by 79.6% between FT1 and FT3. Diet and testing period did not interact (Table 6). Multiple comparisons revealed significant decreases in capture times between FT1 and FT2 ($P = 0.044$) and FT1 and FT3 ($P < 0.001$). Capture times between FT2 and FT3 did not differ ($P = 1.0$).

Fish capture times decreased significantly for the FW group (Table 6). Fish were captured more rapidly at FT2 (90.1%, $P = 0.002$) and FT3 (94.3%, $P = 0.014$) compared with FT1. Worm capture times for the FW-W group decreased between FT1 and FT2 (63.6%) and FT1 and FT3 (53.9%), but the changes were not significant (Table 6). With the exception of the FW-W group, the capture phase was affected by feeding experience more than any other phase.

Prey handling.—Prey handling times decreased slightly for the F group between FT1 and FT2, and increased between FT1 and FT3. Worm handling times by the W group decreased between FT1 and FT2, and between FT1 and FT3 (Table 4), but the changes in handling times for both diet groups were not significant across test periods, and the test by diet interaction was not significant (see Table 6).

For the FW group, fish handling times increased between FT1 and FT2, and between FT1 and FT3, but the changes were not significant overall (Tables 4 and 6). Worm handling times decreased between FT1 and FT2, and between FT1 and FT3,

but no significant changes were found (Tables 4 and 6).

Prey swallowing.—Swallowing times increased across testing periods for the F group, and decreased for the W group (Table 4). Fish swallowing times increased between FT1 and FT2 (22.0%), and between FT1 and FT3 (58.0%). Snakes in the W group swallowed worms more rapidly at FT2 than at FT1 (42.7%), and more rapidly at FT3 than at FT1 (30.5%). However, the changes in swallowing times were not significant (Table 6). The significant interaction between test and diet (Table 6) is due to F group's consistent increase in swallowing times, and the decreased swallowing times for the W group across testing periods.

For the FW group, fish swallowing times were nearly unchanged between FT1 and FT2, and increased between FT1 and FT3 (Table 4), but the differences were not significant (Table 6). Worm swallowing times decreased between FT1 and FT2 and between FT1 and FT3, and these changes were not significant (Table 6).

The Effects of Diet Reversal

Overall consumption times.—Due to snake mortality and food refusal, the sample sizes of the F and W groups diminished considerably between FT4 (181–186 days) and FT5 (226–231 days). Therefore, nonparametric tests (Wilcoxon signed ranks test) were used to compare total consumption times and the feeding phases at FT3 and FT4, and at FT4 and FT5.

The snakes' initial diets influenced their abilities to successfully switch to new prey. At their first feeding on worms (FT4), the snakes in the F group consumed worms as rapidly as the W group snakes did at FT2 (Fig. 2), and consumed them as rapidly as they had fish at FT3 ($Z = 2.67$, $P = 0.79$, Table 7). However, the snakes in the W group were much less successful at making an immediate adjustment to switching from worms to fish (see Fig. 2). Comparing the W group's worm consumption time at FT3 with their first fish test at FT4 revealed a significant increase in the number of seconds taken to consume the prey ($Z = -2.34$, $P = 0.019$). However, they con-

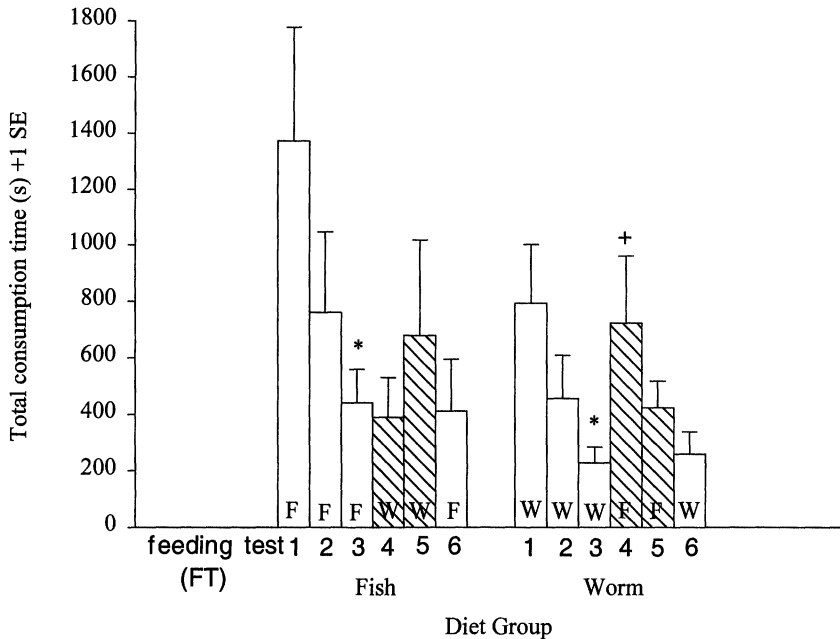


FIG. 2.—Mean (+1 SE) changes in total consumption times as a function of diet (FT1–FT3) and diet reversal (FT4–FT5), and retention for feeding on initial diet (FT3 & FT6) in garter snakes. F = Fish prey, W = Worm prey. At FT4 diets were switched until FT5. Diets then returned to the initial one for FT6. * = $P < 0.01$ significant decrease in total consumption times between FT1 and FT3. + = $P < 0.05$ significant increase in consumption time between FT3 and FT4.

TABLE 7.—Tests for the effects of diet reversal (FT4–FT5) on each feeding phase and total consumption times for snakes in the F (Fish) and W (Worm) groups.

Feeding phase	Diet group	n	M (SE) s at FT4	M (SE) s at FT5	%diff	Z	P
<i>Approach</i>	F	5	682.4 (303.59)	657.6 (499.29)	-3.6	-0.14	0.893
	W	8	542.4 (158.95)	582.0 (204.53)	+7.3	-0.42	0.674
<i>Capture</i>	F	5	128.0 (55.87)	38.0 (21.97)	-70.3	-1.21	0.225
	W	8	633.3 (368.4)	240.6 (93.05)	-62.0	-0.84	0.401
<i>Handle</i>	F	5	21.4 (5.24)	17.4 (6.55)	-18.7	-0.55	0.581
	W	7	111.7 (27.14)	46.9 (11.2)	-58.0	-1.86	0.060
<i>Swallow</i>	F	5	67.0 (10.92)	104.0 (30.86)	+52.2	-0.94	0.345
	W	7	198.4 (28.36)	82.6 (12.1)	-58.4	-2.20	0.028
<i>Total</i>	F	5	216.4 (46.86)	169.6 (27.34)	-21.6	-1.21	0.225
	W	8	919.1 (376.26)	370.9 (87.0)	-59.4	-1.40	0.161

Note: Z = result from Wilcoxon signed ranks tests, P = P-value, FT4 = Feeding test 4, FT5 = Feeding test 5. FT4 was the first feeding test for the snakes on the reversed diet, and FT5 was the last test on the reversed diet, completed after 11 or 12 feedings.

TABLE 8.—Tests for retention of feeding skills in snakes from the F (Fish) and W (Worm) groups. Tests compare feeding phases and total consumption times at FT3 and FT6.

Feeding phase	Diet group	n	Mean (SE) s at FT3	Mean (SE) s at FT6	%diff	Z	P
<i>Approach</i>	F	8	505.3 (168.42)	287.4 (121.66)	-43.1	-1.26	0.208
	W	12	447.7 (164.86)	296.5 (108.38)	-33.8	-0.86	0.388
<i>Capture</i>	F	8	316.0 (112.23)	232.0 (185.44)	-26.6	-0.98	0.327
	W	12	134.5 (60.32)	163.7 (80.8)	+21.7	-0.08	0.937
<i>Handle</i>	F	8	52.8 (19.26)	79.4 (41.56)	+50.4	-0.49	0.624
	W	12	31.6 (10.09)	17.1 (3.92)	-45.9	-1.49	0.136
<i>Swallow</i>	F	8	107.9 (24.63)	99.4 (22.97)	-7.9	-0.28	0.779
	W	12	67.8 (11.41)	80.6 (18.2)	+18.9	-0.63	0.530
<i>Total</i>	F	8	476.6 (120.81)	410.8 (183.45)	-13.8	-0.56	0.575
	W	12	233.8 (65.78)	261.3 (84.44)	+11.8	0.00	1.0

Note: Z = result from signed ranks test, P = P-value, FT3 = Feeding test 3, FT6 = Feeding test 6. FT3 was the last feeding test completed for snakes feeding on their initial diet, and FT6 was done following the diet reversal period.

sumed fish more rapidly at FT4 (39.4%) than the snakes in the F group at their first feeding test with fish (FT1, see Fig. 2 and Table 7). This suggests that feeding on worms may have partially facilitated the snakes' ability to switch to a new diet. However, this comparison is confounded by maturational factors (e.g., physical development). The W group benefited from fish feeding experience, as shown by the 59.4% decrease in consumption time between FT4 and FT5, but this difference was not significant. This may be due to the fact that they were consuming fish as rapidly as possible given their body sizes and levels of feeding experience.

Comparisons by Feeding Phase

Descriptive statistics and statistical comparisons for each feeding phase are provided in Table 7. Snakes in the F group showed a slight decrease in worm approach time and the W group slightly increased their fish approach times by 7.3%, but the changes were not significant. Decreases in worm capture times by the F group and fish capture times by the W group were not significant (Table 7). Worm handling times barely changed for

the F group and the W group handled fish more rapidly at FT5 than at FT4, but neither change was statistically significant. Worm swallowing times actually increased for the F group, but the change was not significant, and fish swallowing times decreased significantly (58.4%) for the W group (Table 7).

Retention of Feeding Skills

Total consumption times.—Reversing the diets of the F and W groups did not appear to affect their abilities to detect and consume the prey on which they had initially fed. Total prey consumption times between FT3 and FT6 did not significantly change for either diet group (see Fig. 2, Table 8). Fish consumption times slightly decreased between FT3 and FT6, and worm consumption times increased slightly, but the changes were not significant.

Comparisons by Feeding Phase

The snakes showed no deterioration of ability to detect their first experienced prey. Approach latencies between FT3 and FT6 decreased for the F and W groups, but the changes were not significant (Table 8). Capture times also remained relatively

unchanged between FT3 and FT6 for the F and W groups. Fish handling times increased for the F group, and worm handling time decreased, but neither change was significant. Swallowing times also did not significantly change between FT3 and FT6 for the F and W groups.

DISCUSSION

Experience played an important role in the development of feeding abilities in garter snakes through the first 8 months, and the changes that took place seemed relatively permanent. Physical maturation certainly may contribute to improved foraging skills, but the body and head sizes of the snakes in each diet group did not significantly differ during this study (Krause, 2000), and test prey were always measured to within 10–15% of each snake's body weight for all feeding tests. The importance of feeding experience was especially evident during the first 40 to 45 days, as evidenced by marked decreases in prey consumption times between FT1 and FT2. Figures 1 and 2 show how drastic the decreases in total consumption times were between FT1 and the remaining tests for all diet groups. However, initial diet influenced the snakes' abilities to switch to new prey items. Feeding on fish, which can be relatively difficult for neonatal *T. sirtalis* to consume (Halloy and Burghardt, 1990), may facilitate switching to prey such as worms (see Fig. 2). Feeding on worms may have impeded the W group's ability to switch to fish, as prey consumption times increased significantly between FT3 and FT4 for this group. After 11 to 12 feedings on fish, the W group decreased its mean fish consumption time to a level comparable to the F group at FTs 1 and 2. Therefore, feeding experience played an important role in the ontogeny of feeding skills beyond the first 40 to 45 days. It is unlikely that morphological differences accounted for the facilitation and interference effects found in the F and W groups, respectively. The snakes in the two diet groups did not significantly differ in SVL, mass, or head dimensions when diet switching took place (Krause, 2000).

This experiment extends the findings of

Burghardt and Krause (1999), where neonatal *T. sirtalis* were tested at birth and after 11 or 12 feedings. It appears that, with the exception of the W group's first feeding on fish, prey consumption times reach their lowest levels for young garter snakes after only 11 or 12 feedings. Also, similar to the results reported by Burghardt and Krause (1999), prey consumption phases were differentially affected by feeding experience.

On average, prey approach latencies decreased across feeding tests, but the changes were not significant. This result was unexpected, given the significant decreases in prey approach latencies for the F and W groups tested in Burghardt and Krause (1999). This difference between the two studies may be due to the lower sample size used in the present study. Although there was a general trend toward decreasing prey approach latencies, the variability was much more substantial for approach latencies than in Burghardt and Krause (1999). Environmental conditions were nearly identical, and the same observer recorded data in both studies, thus ruling out the possibility of differences due to room temperature, caging, or the data recorder. One notable difference is that different species of fish were used in the two studies. The fish used by Burghardt and Krause (1999) were mosquito fish (*Gambusia affinis*), which has a dark dorsum and a white/gray underside. Due to low availability of *Gambusia* at the time of this study, we used fathead minnows (*Pimephales promelas*) instead, which were a special strain that had a light orange dorsum and a white/gray underside. Fish were size matched in proper proportions to snake body sizes, but the differences in coloration may have had different effects on approach latencies. However, this does not explain why approach latencies to worms did not decrease with feeding experience in this study. Motivational factors are unlikely, since snakes in both studies were tested at the same ages.

The snakes in the F, W, and FW-F group decreased their capture times significantly between FT1 and FT3. Burghardt and Krause (1999) report the same

result in their study. Table 4 shows that the amount of time taken to capture prey exceeded that of handling and swallowing prey. Decreased capture times accounted for the majority of the reductions in total consumption times between feeding tests for each diet group. Chemosensory detection of prey, as well as visual and tactile cues probably interact as prey capturing skills develop. *T. sirtalis* uses a fairly unspecialized tactic for capturing fish. When preying upon fish, aquatic specialist species such as *T. melanogaster* and *T. couchii* rely heavily on visually guided and directed strikes toward prey, whereas *T. sirtalis* uses an "open-mouth search" tactic (Drummond, 1983; Halloy and Burghardt, 1990). The open-mouth search is characterized by lateral movements of the head with the jaws open (Drummond, 1983; Savitsky and Burghardt, 2000), and prey seizure is probably facilitated by tactile and visual cues. In contrast to *T. melanogaster*, fish capturing tactics by neonatal *T. sirtalis* appear indiscriminate, as orientation toward prey is much less direct and precise. However, fish capture times decreased significantly in Experiment I of this study, and Halloy and Burghardt (1990) report superior fish capturing abilities by adult *T. sirtalis* in comparison to yearling and neonatal conspecifics.

In this study, we did not systematically record whether open-mouth searching occurred. However, open-mouth searching was observed quite frequently among the snakes in the F and FW-F groups at their first feeding trials. Open-mouth searching by the neonates was prolonged on occasion, and often resulted in the snakes withdrawing from the water dish, especially if prey remained motionless and direct contact was not made. With feeding experience, it appeared that open-mouth searching became more directed and fewer lateral head movements were made. Unfortunately we can not provide much detail on this aspect of prey capturing behavior, but further work could closely examine the ontogeny of open-mouth searching behavior by *T. sirtalis*.

Worm swallowing times by the W and FW-W groups decreased in the present

study, but not significantly. Burghardt (1978) recorded worm-swallowing latencies by 13 newborn *T. sirtalis*, and found a consistent and rapid decline in swallowing times during each of their first 8 feedings. The W group in Burghardt and Krause (1999) significantly reduced the time it took to swallow worms. However, the swallowing times reported in Burghardt and Krause (1999) were greater at their initial feedings (131.2 s) than in the present study (66.8 s). Comparisons of fish swallowing times for the F groups of both studies are complicated by the fact that different fish species were used in Burghardt and Krause (1999) and in this Experiment. The fathead minnows generally took longer to swallow, probably due to different head sizes of the two species.

As hypothesized, the snakes showed no decrement in feeding skills for their initial prey following food switching. Comparisons between FT6 and FT3 for both diet groups yielded no significant changes in total consumption times or any of the feeding phases. Thus, it appears that experience plays a long lasting role in the early ontogeny of predatory behavior in *T. sirtalis*. This result also confirms that prey consumption times asymptote for snakes of this age. However, the amount of feeding experience on the initial diet versus the reversed diet was unbalanced. The snakes in the F and W groups had twice as much experience feeding on their initial prey species than they had with a new species. Including prey eaten during the feeding tests, the snakes in both groups had at least 25 meals (1 prey item/meal) between FT1 and FT3, and an average of only 13 meals (1 prey item/meal) on the reversed diet (FT4–FT5). The results comparing FT3 and FT6 may have differed had the snakes eaten an equal number of meals on the reversed diet. Furthermore, the high mortality between birth and 8 months reduced the sample size considerably between FT1 and FT6. The generality of our findings may be limited since the group of snakes that completed all feeding tests may not comprise an adequate representative sample.

TABLE 9.—Mean (± 1 SE) SVL, body weight, and total number of feeding tests completed for each prey item by males and females from Miller's marsh (MM) and McCafferty farm (MF).

Site		SVL (mm)	Weight (g)	Prey		
				Fish	Frog	Worm
MM	Males ($n = 22$)	441.6 (10.2)	33.9 (2.1)	9	2	11
	Females ($n = 22$)	497.4 (17.2)	58.7 (6.3)	6	8	8
MF	Males ($n = 9$)	481.7 (12.8)	49.2 (2.9)	4	0	5
	Females ($n = 20$)	512.9 (14.8)	68.8 (5.0)	3	9	8

EXPERIMENT II: SITE VARIATION IN ADULT PREDATORY SKILLS

With some exceptions, feeding experience resulted in significant decreases in prey consumption times for the snakes tested in Experiment I, and these decreases were often related to the type of prey consumed. If feeding experience has long term effects on adult predatory behavior, then differences in consuming prey should reflect differences in natural diets. If differences exist in the abilities of the adult snakes from the two sites to capture and consume prey, these could be due to either genetic differences between the sites or to the feeding histories of the individual snakes (Burghardt and Schwartz, 1999). Due to the close proximity of the two sites and the lack of any site differences in neonatal behavior, we reasoned that any differences in prey feeding skills would be due to experience rather than to genotypic differences between sites.

MATERIALS AND METHODS

During May and June, 1999, 70 wild-caught adult garter snakes from both sites (Miller's marsh, $n = 41$ snakes; McCafferty farm, $n = 29$ snakes) were captured by hand and brought to the Biological Station. The snakes were sexed, weighed, measured (see Table 9) and scale clipped for later identification. All stomach contents were removed by gently palpating each snake's abdomen with the thumb. If ingested prey were detected, stomach contents were removed by gently pushing the prey forward through the stomach and gullet. Snakes were group housed by site, and water was available *ad libitum*. Temperature was kept at 20–25 C, and the snakes were housed near windows to keep them as close to their natural light:dark

cycles as possible. Each snake was assigned to one feeding condition: Fish, Worm, or Frog. This was done randomly, with the constraint of balancing as best as possible across sex and site. Banded killifish (*Fundulus diaphanus*) were captured by seine along the north shore of Beaver Island, green frogs (*Rana clamitans*) were captured with dip nets from various ponds near the Biological Station, and earthworms (*Lumbricus terrestris*) were obtained from a local bait supplier.

Snakes were allowed to acclimate to captivity for three to five days prior to testing. This, along with stomach content removal, also served to standardize hunger levels as much as possible. One hour prior to testing, each snake was placed in a clear plastic cage (29 × 41 × 16 cm), with a paper towel substrate. Data were collected live using the same behavioral measures as for neonates in Experiment I (see Table 2). Prey were weighed to the nearest 0.1 gram and placed into clear plastic bowls (150 × 65 mm) with an opaque paper strip surrounding the outside of the bowl to minimize visual cues.

The banded killifish was the largest species of fish that could be consistently captured by seine along the island shore. The fish offered were on average 8.0% (SE = $\pm 0.01\%$) of snake body masses. Worm body weights were on average 9.0% (SE = $\pm 0.01\%$) of snake body masses. The species of frog used for testing, and the body sizes of individual frogs, were chosen based on availability. The snake-prey body-size proportions of the frogs were not the same as those for fish and worm prey. Frogs of comparable sizes to fish and worms were not consistently found at Miller's marsh or in ponds near the biological station. Adult green frogs were abundant

TABLE 10.—Mean (± 1 SE) differences (in s) among each prey type for all feeding phases and total consumption times for wild-caught adult garter snakes from Miller's marsh (MM) and McCafferty farm (MF).

		<i>n</i>	Approach mean (SE)	Capture mean (SE)	Handle mean (SE)	Swallow mean (SE)	Total mean (SE)
<i>Fish</i>	MM	15	594.5 (103.4)	399.4 (108.0)	53.3 (12.2)	88.1 (16.2)	540.8 (109.5)
	MF	7	231.4 (75.9)*	315.9 (65.3)	64.6 (38.1)	130.0 (60.2)	510.4 (146.2)
	Mean		413 (89.7)	357.7 (86.7)	59.0 (25.2)	109.1 (38.2)	525.6 (127.9)
<i>Worm</i>	MM	19	711.6 (145.3)	112.6 (55.2)	13.7 (3.3)	49.7 (5.7)	170.3 (53.5)
	MF	13	264.7 (60.5)*	77.5 (41.3)	10.3 (2.2)	90.2 (15.8)*	178.0 (41.9)
	Mean		488.2 (102.9)	95.1 (48.3)	12.0 (2.75)	70.0 (10.8)	174.2 (47.7)
<i>Frog</i>	MM	10	437.8 (162.6)	376.0 (146.6)	669.1 (268.5)	1045.7 (315.0)	1950.2 (502.3)
	MF	9	344.8 (96.1)	1000.0 (889.3)	603.8 (143.7)	1209.3 (169.8)	2496.2 (1019.4)
	Mean		391.3 (129.4)	688.0 (518.0)	636.5 (206.1)	1127.5 (242.4)	2223.2 (760.9)

Note: * = $P < 0.05$ difference between sites.

enough during the study period to use for testing. Frog body weights were on average 27.0% (SE = $\pm 0.02\%$) of snake body masses.

Bowls holding fish or frog prey were half filled with water, with a shallow layer of gravel at the bottom. Worms were placed in a shallow layer of dirt. To prevent the prey from escaping, lids were placed on top of the bowls with an opening (80 mm diameter) cut in the center so that the snakes could enter (and chemical cues could escape). If prey were not captured within one hour, trials were terminated and repeated the following day. Snakes that did not eat after three trials were released.

Statistical Tests

A MANCOVA was used to test for the effects of prey type (prey) on each feeding phase, and on the total amount of time to feed. Sex, site, and prey were treated as fixed factors. To control for the effects of snake and prey body sizes on all measures, SVL and prey weight were treated as covariates. No significant effect for sex was found so this factor was dropped from the model. Pairwise comparisons were used to compare differences in each phase and total consumption times among prey types. Descriptive statistics of non-transformed values revealed several outliers beyond 3 standard deviations, and the assumption of homogeneity of variances was not met for several measures. Transforming the data using natural log (+1) transformations resulted in normalized data with equal variances.

RESULTS

Overall Prey, Sex, and Site Effects

Descriptive data were gathered for each feeding phase as well as total consumption times for each prey type for snakes from both sites (Table 10). SVL was a significant covariate ($\lambda = 0.67$, $F_{5,52} = 5.16$, $P = 0.001$), as was prey mass ($\lambda = 0.64$, $F_{5,52} = 5.98$, $P < 0.001$). SVL significantly covaried with capturing, swallowing and total consumption time. Prey weight significantly covaried with all phases except for approach time. A marginally significant effect was found for site ($\lambda = 0.83$, $F_{5,52} = 2.11$, $P = 0.078$) and a significant effect was found for prey ($\lambda = 0.31$, $F_{10,104} = 8.26$, $P < 0.001$). The univariate tests on each phase and total consumption times for each factor gave similar results (Table 11). The significant site effect is explained by differences in swallowing times. Snakes from McCafferty farm took longer to swallow all three prey types. However, the snakes from McCafferty farm approached prey more quickly than did the snakes from Miller's marsh (Table 10).

Pairwise comparisons were made to determine which feeding phases differed among prey types (Table 12). Mean latencies to capture, handle and completely consume fish were significantly longer than for worms, but approach latencies and swallowing times did not differ. Frogs took significantly longer to handle, swallow, and completely consume than both fish and worms. Worm capture times were significantly faster than frog capture times. These results were not due to differences

TABLE 11.—Results of *F*-tests for Site and Prey effects on each feeding phase and total consumption times in wild-caught garter snakes from Miller's marsh ($n = 44$) and McCafferty farm ($n = 29$).

Source	DV	df	MS	<i>F</i>	<i>P</i>
Covariate (SVL)	Approach	1	2.88	2.72	0.105
	Capture	1	7.33	4.60	0.036
	Handle	1	0.54	0.53	0.472
	Swallow	1	4.45	14.10	<0.001
	Total	1	4.95	10.41	0.002
Covariate (prey weight)	Approach	1	0.45	0.43	0.517
	Capture	1	15.43	9.69	0.003
	Handle	1	6.36	6.14	0.016
	Swallow	1	4.97	15.77	<0.001
	Total	1	1.05	18.36	<0.001
Site	Approach	1	3.48	3.29	0.075
	Capture	1	4.70E-02	0.03	0.864
	Handle	1	0.64	0.62	0.434
	Swallow	1	1.81	5.74	0.020
	Total	1	0.24	0.51	0.476
Prey	Approach	2	2.0E-02	0.02	0.981
	Capture	2	25.37	15.93	<0.001
	Handle	2	16.35	15.79	<0.001
	Swallow	2	5.78	18.33	<0.001
	Total	2	11.45	24.08	<0.001
Site × Prey	Approach	2	1.27	1.20	0.310
	Capture	2	0.243	0.15	0.859
	Handle	2	0.191	0.18	0.832
	Swallow	2	5.72E-02	0.18	0.835
	Total	2	2.23E-02	0.05	0.954
Error	Approach	56	1.06		
	Capture	56	1.59		
	Handle	56	1.04		
	Swallow	56	0.32		
	Total	56	0.48		

in relative head sizes, as head length was not a significant covariate.

Site Effects

A second MANOVA compared all measures for each prey type separately, with site as a grouping variable. Sex was not a significant factor for any of these tests and was dropped from the model. SVL and prey weight were treated as covariates.

Fish.—Overall, SVL significantly covaried with the amount of time taken to consume fish ($\lambda = 0.28$, $F_{5,14} = 7.29$, $P = 0.001$). All feeding phases were significantly affected by SVL except for approach latency (Table 13). Prey weight was also a significant covariate ($\lambda = 0.32$, $F_{5,14} = 5.84$, $P = 0.004$), with swallowing and total consumption times significantly affected by prey weight (Table 13). A significant effect for site was found for fish prey ($\lambda = 0.30$, $F_{5,14} = 6.52$, $P = 0.002$). Although snakes from both sites captured,

and swallowed fish with equal proficiency (see Table 13), the snakes from McCafferty farm approached fish more rapidly than did the snakes from Miller's marsh. Total fish consumption times did not differ between the two sites.

Worm.—SVL covaried with the amount of time taken to consume worms ($\lambda = 0.49$, $F_{5,23} = 4.73$, $P = 0.004$), but prey weight was not a significant covariate ($\lambda = 0.79$, $F_{5,23} = 1.19$, $P = 0.345$). A significant site effect was found for worm prey ($\lambda = 0.36$, $F_{5,25} = 2.85$, $P = 0.036$). The snakes from McCafferty farm approached worms more rapidly than the snakes from Miller's marsh, but the latter swallowed worms more rapidly (Table 10). Total worm consumption times did not differ between snakes from the two sites (Table 13).

Frog.—Snout-vent length did not covary with times taken to consume frogs ($\lambda = 0.34$, $F_{5,3} = 1.18$, $P = 0.474$). Prey weight was not a significant covariate ei-

TABLE 12.—Pairwise comparisons between each prey species for all feeding phases and total consumption times by wild-caught garter snakes from Miller's marsh and McCafferty farm. All significant *P*-values are boldfaced.

Feeding phase	Worm		Frog		
	Mean diff (s) fish-worm	<i>P</i> value	Mean diff (s) fish-frog	<i>P</i> value	
<i>Fish</i>	Approach	-75.2	1.0	21.7	1.0
	Capture	262.6	< 0.001	-330.3	1.0
	Handle		< 0.001	-577.5	< 0.001
	Swallow	47.0	0.174	-1018.4	< 0.001
	Total	39.1	< 0.001	-1697.6	< 0.001
		351.4			
			<i>Worm-frog</i>		
<i>Worm</i>	Approach	—	—	96.9	0.414
	Capture	—	—	-592.9	0.011
	Handle	—	—	-624.5	< 0.001
	Swallow	—	—	1057.5	< 0.001
	Total	—	—	-2049.0	< 0.001

ther ($\lambda = 0.40$, $F_{5,3} = 0.90$, $P = 0.574$). Overall, site was not a significant factor for frog prey ($\lambda = 0.34$, $F_{5,5} = 0.52$, $P = 0.755$), and there were no differences for any of the feeding phases or total frog consumption times between the two sites (Table 13).

DISCUSSION

The worm only diet of the adult snakes from McCafferty farm apparently has no effect on their abilities to handle large bodied and difficult to handle prey such as frogs, and novel prey such as fish. The faster swallowing times, especially for worms, by the snakes from Miller's marsh may be due to their normally feeding upon larger prey. Morphological differences are unlikely to account for the quicker swallowing times by the snakes from Miller's marsh, as head size variation between sites was minimal (Krause, 2000). Also, the species of earthworm used in this experiment is not native to Beaver Island and is much larger than are the native worms. Thus, the snakes from Miller's marsh may have had a slight advantage in worm swallowing performance over the snakes from McCafferty farm. Indeed, experience with more difficult prey (fish and frogs) may facilitate swallowing of less difficult prey, and swallowing time was the only overall site difference found (Table 11), with the snakes from Miller's Marsh swallowing all

prey faster than McCafferty Farm snakes (Table 10).

The results from this experiment must be treated as tentative, as appropriate methods (e.g., radio telemetry) have not been implemented to determine the full wandering range of garter snakes at McCafferty farm. It is possible that McCafferty farm snakes have migrated to and from sites where amphibians are available. However, given their smaller mean body sizes (Krause, 2000) and because gut contents have consisted only of worms from several field seasons since 1991 (Gillingham and Burghardt, unpubl.), it is fairly safe to assume that these snakes primarily consume worms. Furthermore, Graves et al. (1993) recorded home range use by *T. sirtalis* at Jordan River, a site near McCafferty farm were the snakes also specialize on earthworms, and found that healthy adult snakes remained near their capture sites and moved an average of only 40.4 m/day. If the home range usage by the McCafferty farm snakes is comparable to the Jordan River snakes, they would not encounter habitat similar to Miller's marsh.

In light of the results from Experiment I, the long-term importance of feeding experience on prey capture and handling may not be dependent upon the type of prey consumed. Adult snakes from McCafferty farm were equally proficient at

TABLE 13.—Results of *F*-tests for Site effects on each feeding phase and total consumption times for each prey type.

Prey	Source	DV	df	MS	<i>F</i>	<i>P</i>
<i>Fish</i>	Covariate (SVL)	Approach	1	0.24	0.28	0.601
		Capture	1	4.50	5.27	0.034
		Handle	1	5.38	4.65	0.045
		Swallow	1	5.38	28.28	< 0.001
		Total	1	4.53	10.99	0.004
	Covariate (prey weight)	Approach	1	0.43	0.51	0.484
		Capture	1	0.72	0.84	0.372
		Handle	1	1.60	1.38	0.255
		Swallow	1	6.50	34.16	< 0.001
		Total	1	1.95	4.73	0.043
	Site	Approach	1	5.36	6.42	0.021
		Capture	1	0.66	0.78	0.389
		Handle	1	0.27	0.23	0.636
		Swallow	1	0.64	3.35	0.084
		Total	1	0.25	0.61	0.446
	Error	Approach	18	0.84		
		Capture	18	0.85		
		Handle	18	1.16		
		Swallow	18	0.19		
		Total	18	0.41		
<i>Worm</i>	Covariate (SVL)	Approach	1	9.32	10.01	0.004
		Capture	1	1.86	1.05	0.314
		Handle	1	3.44E-03	0.01	0.942
		Swallow	1	1.11	3.78	0.062
		Total	1	1.61	2.82	0.105
	Covariate (prey weight)	Approach	1	3.30	3.55	0.070
		Capture	1	0.57	0.32	0.574
		Handle	1	2.70E-04	0.01	0.984
		Swallow	1	5.94E-02	0.20	0.656
		Total	1	0.28	0.50	0.488
	Site	Approach	1	7.33	7.87	0.009
		Capture	1	0.16	0.09	0.765
		Handle	1	0.44	0.68	0.417
		Swallow	1	1.50	5.12	0.032
		Total	1	0.15	0.27	0.609
	Error	Approach	27	0.93		
		Capture	27	1.77		
		Handle	27	0.64		
		Swallow	27	0.29		
		Total	27	0.57		
<i>Frog</i>	Covariate (SVL)	Approach	1	0.14	0.08	0.780
		Capture	1	0.74	0.21	0.664
		Handle	1	5.89	4.55	0.070
		Swallow	1	2.25E-02	0.16	0.704
		Total	1	9.29E-02	0.41	0.540
	Covariate (prey weight)	Approach	1	0.20	0.12	0.739
		Capture	1	4.27	1.18	0.313
		Handle	1	1.17	0.90	0.373
		Swallow	1	0.39	2.72	0.143
		Total	1	0.39	1.73	0.230
	Site	Approach	1	4.67E-02	0.03	0.872
		Capture	1	3.71E-03	0.01	0.975
		Handle	1	0.82	0.63	0.452
		Swallow	1	0.22	1.54	0.254
		Total	1	7.41E-05	0.01	0.986
	Error	Approach	7	1.66		
		Capture	7	3.60		
		Handle	7	1.29		
		Swallow	7	0.14		
		Total	7	0.22		

consuming frogs, presumably a novel prey type, as snakes from Miller's marsh. The same applied to feeding on worms, which are common to both sites, and fish, which are not present at either site. Based on Experiment I, and on Burghardt and Krause (1999), the primary hypothesis that we tested in Experiment II was that, based on their presumed feeding histories, snakes from Miller's marsh would handle frogs and fish more proficiently than snakes from McCafferty farm. Approach latencies to frogs were equal for snakes from both sites, suggesting that motivational factors were not a factor for this prey species. However, adult snakes from McCafferty farm approached worms and fish more rapidly than the snakes from Miller's marsh, but capture times were not significantly different. Differences in reactivity could account for the slower approach times by the snakes from Miller's marsh.

Although feeding experience plays an important role in the ontogeny of feeding by young *T. sirtalis* (Burghardt and Krause, 1999; Halloy and Burghardt, 1990; Experiment I of this study), when adult body size is reached, it may be that prey size determines the amount of time taken to consume prey. Perhaps prey specific experience only manifests itself in a narrow range of relative prey sizes. In addition, the anti-predator behavior of prey may constrain the tactics that predators can use in capturing, handling, and swallowing their prey. That the snakes from McCafferty farm consumed frogs with equal proficiency to the snakes from Miller's marsh suggests that this may be the case. All frogs were swallowed rear end first, and no attempts at head-first ingestion were observed. The large body sizes of the frogs, and presumably their relatively high levels of strength, appear to require that the snakes subdue the posterior (leg) region of the frogs to prevent escape. Snakes from both sites did this on each trial in which frogs were eaten. If tested on dead (or smaller) frogs, the snakes from Miller's marsh may have handled and swallowed their prey more rapidly than the snakes from McCafferty farm. Captive *T. sirtalis* will consume dead prey (Arnold, 1978),

and may scavenge in the field when provided the opportunity. However, consumption of live prey by wild *T. sirtalis* is probably much more frequent, and the ecological validity of Experiment II was increased with the use of live prey. Testing the snakes in laboratory conditions may have compromised the ecological validity of Experiment II. Foraging in aquatic habitats such as Miller's marsh may require skills that could not be expressed in our laboratory tests, such as detecting and subduing prey underwater.

GENERAL DISCUSSION

Snakes and other reptiles have an often overlooked capacity to learn (see Burghardt, 1977). In Experiment I, neonatal garter snakes improved their foraging skills with feeding experience. There are many kinds of learning, though, and these must be related to the ecological and evolutionary histories of the organisms studied (Shettleworth, 1998). The studies reviewed by Burghardt (1977) primarily covered operant, associative, and maze learning in many species of reptiles. Spatial learning and memory have been systematically studied in several reptilian species (see Day et al., 1999; Holtzman et al., 1999, refs. therein). Ford and Burghardt (1993) review ecologically relevant research examining several types of learning in reptiles, including chemosensory identification of prey and predator avoidance.

Learning to detect, capture and consume prey encompasses a variety of sensory and behavioral changes. For example, the improvements in prey capturing abilities by the F, W, and FW groups in Experiments I presumably required the integration of chemical, visual, and tactile senses (although the predominant modality was not determined). The natural history of *Thamnophis sirtalis*, with their broad geographical distribution and diverse diets, suggests that the benefits of being a dietary generalist far outweigh the costs. Their propensity to attack a wide variety of prey (Burghardt, 1969), and their abilities to rapidly acquire foraging skills on new prey, suggest that behavioral plas-

ticity in *T. sirtalis* is a primary factor in their success as a species.

Because live prey were used, the behavior of the fish and worms probably affected the results of both experiments. Capture times may have decreased across test periods in Experiment I because the snakes were better able to detect prey movements with feeding experience. Burghardt and Denny (1983) found that prey movement, in addition to chemical cues, is an important factor that elicits predatory responses in *T. sirtalis*. Handling and swallowing times are almost certainly affected by whether prey are alive or dead. Decreases in handling and swallowing times may be facilitated by the snakes' familiarity with how prey attempt to escape. Future work could compare the acquisition of feeding skills by snakes feeding on live or dead prey. Also, identifying changes and integration among sensory modalities (e.g., chemical, visual, tactile) as feeding skills increase would provide further, and more detailed, explanation for the development of successful foraging. Diets and test prey were randomly assigned without consideration of individual prey preferences in Experiments I and II respectively. Feeding experience and exposure to prey chemicals are known to alter prey preferences in *T. sirtalis* (Burghardt, 1992). Congenital and experience-based prey preferences were not tested in Experiments I and II of this study, but are important sources of plasticity of snake foraging behavior.

The Retention of Feeding Skills

Following diet switching, the snakes did not show any decrement in feeding skills for prey comprising their initial diet. The concept of a 'memory window' has been developed by several investigators studying foraging behavior (e.g., Cuthill et al., 1990; Hughes et al., 1992; Valone, 1992). The 'memory window' refers to the "... duration of learned information or skills, for example in relation to food caches, harvest rate, prey handling time, or recognition of potential predators" (Mackney and Hughes, 1995, p. 1241). Memory for prey toxicity could be added to this list, and has in fact been demonstrated in garter snakes

(Burghardt et al., 1973; Terrick et al., 1995).

The memory window for prey feeding skills by young *T. sirtalis* appears to be at least 10 weeks, as feedings at FT6 were done with the same proficiency as feedings on the same prey at FT3 (Experiment I). The memory window for prey feeding skills is most likely much larger and warrants further study. Also, comparisons between generalist and specialist snake species could be made. Memory windows for feeding on novel, atypical prey may be greater in *T. sirtalis* than in more specialized species such as *T. melanogaster*, or *T. butleri*.

Memory can be viewed from a functional, adaptive perspective. For example, Anderson and Schooler (1991) suggest that the probability of retrieving encoded information should be equal to the probability of the information being needed again. Experiments testing this hypothesis have largely been conducted with human subjects (e.g., Anderson, 1991), but the relationship between event recurrence and retrieval probabilities can be applied to nonhuman species (see Shettleworth, 1998). So far, the majority of the literature dealing with this relationship seems to be on memory for seed cache storage in birds (see Balda et al., 1998; Kamil and Roitblat, 1985). Herzog (1990) found that young garter snakes that were briefly exposed to a predator model on seven occasions showed greater tendencies to flee weeks afterward. Snakes, especially generalist species, may encounter seasonal fluctuations in prey availability, abundance, or dispersal patterns, and hibernation results in extensive periods without feeding experience. Snakes that are able to retain their abilities to detect, capture, and efficiently consume prey upon each encounter may suffer less from predation, and may be better able to diversify their diets.

Early Feeding Experience and Survival

Although experience may not affect long-term prey-specific foraging efficiency in these garter snakes, feeding experience appears to play a very important role in the development of foraging skills in young

garter snakes. Lind and Welsh (1994) report age-related differences in diet and foraging behavior in wild *Thamnophis atratus*, indicating that an ontogenetic shift in feeding behavior occurs during early adulthood. The role of feeding experience and learning when undergoing such shifts is in need of further research. In addition to feeding behaviors, snakes are known to undergo ontogenetic shifts in preferred habitat during foraging. Savitsky and Burghardt (2000) found that young water snakes (*Nerodia rhombifer*) forage in highly vegetated areas near shallow water, whereas adult water snakes frequently forage in the open water where predation risk may be higher. Predator pressure may differentially affect habitat selection by snakes of different size classes. Neonatal survival rates may increase through the selection of foraging habitats where predation risks are minimized and by improving foraging skills through learning.

In comparison to snakes, the development of predation in mammals is characterized by long periods of experience, where observational learning, play, social competition, and practice all may facilitate the ontogeny of adult predatory skills (Caro, 1980; Polsky, 1975; Vargas and Anderson, 1998). Precocial species with no maternal care, such as *T. sirtalis*, rely on feeding experience and maturation by physical growth to facilitate the development of foraging skills. Neonatal *T. sirtalis* may often be born into unpredictable and fluctuating environments. For a precocial predatory generalist, it may pay to be relatively unspecialized at birth, and yet have the capacity to develop foraging capacities that are comparable to specialist species (e.g., Mori, 1996) after only a limited amount of feeding experience.

The capacity to rapidly acquire feeding skills may be especially beneficial to a species that is subject to high levels of neonatal predation. Lawton and Hughes (1985) and Brown and Richardson (1987) found that the foraging behavior of muricid gastropods and predatory crabs is greatly influenced by mortality risks, and that foraging skills are rapidly acquired with feeding experience. Snake survival

rates in the wild are difficult to quantify. Mortality seems to be fairly high for wild neonatal *T. sirtalis* (Jayne and Bennett, 1990). Snakes may be especially vulnerable to predation while foraging in areas without cover, underwater, or along water banks. Young *T. sirtalis* moving into such areas may be especially susceptible to predation. Learning and remembering how to rapidly detect, capture, handle, and swallow prey would be beneficial for a species with high neonatal and juvenile mortality due to predation, and would further facilitate the invasion of new habitats and feeding niches.

Heritabilities for physiological, morphological, and behavioral traits associated with anti-predator and foraging behavior by *T. sirtalis* have been widely studied (Arnold, 1981; Arnold and Bennett, 1988; Burghardt and Schwartz, 1999; see Brodie and Garland, 1993, for review). Measuring selection on these traits in the wild is extremely difficult. However, Jayne and Bennett (1990) assayed several important morphological and behavioral traits associated with predator encounters, and determined that some of these served as important predictors of survival in the wild. Thus, there is probably strong selection acting on traits such as scalation patterns, locomotor abilities, striking, reversing direction of travel, and fleeing. Similarly, if there is high predation on foraging *T. sirtalis* neonates, there may be selection for the rapid acquisition of feeding skills. Litter effects were found for capture and total consumption times at FT1 of Experiment I, and Burghardt and Krause (1999) found litter effects for various prey consumption latencies. Further work could examine the relationship between the acquisition of predatory skills and survival in the wild by *T. sirtalis*.

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LITERATURE CITED

- ANDERSON, J. R. 1991. Is human cognition adaptive? *Behavioral and Brain Sciences* 14:471–517.
- ANDERSON, J. R., AND L. J. SCHOOLER. 1991. Reflections of the environment in memory. *Psychological Science* 2:396–408.
- ARNOLD, S. J. 1978. Some effects of early experience on feeding responses in the common garter snake, *Thamnophis sirtalis*. *Animal Behaviour* 26:455–462.
- . 1981. Behavioral variation in natural populations. I. Phenotypic, genetic, and environmental correlations between chemoreceptive responses to prey in the garter snake, *Thamnophis elegans*. *Evolution* 35:489–509.
- . 1992. Behavioural variation in natural populations. VI. Prey responses by two species of garter snakes in three regions of sympatry. *Animal Behaviour* 44:705–719.
- ARNOLD, S. J., AND A. F. BENNETT. 1984. Behavioural variation in natural populations, III. Antipredator displays in the garter snake, *Thamnophis radix*. *Animal Behaviour* 32:1108–1118.
- BALDA, R. P., I. M. PEPPERBERG, AND A. C. KAMIL (Eds.). 1998. *Animal Cognition in Nature*. Academic Press, San Diego.
- BRODIE, E. D., AND T. GARLAND. 1993. Quantitative genetics of snake populations. Pp. 315–362. In R. A. Siegel and J. T. Collins (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, New York.
- BROWN, K. M., AND T. D. RICHARDSON. 1987. Foraging ecology of the southern oyster drill *Thais haemastoma* (Gray): Constraints on prey choice. *Journal of Experimental Marine Biology and Ecology* 114:123–141.
- BURGHARDT, G. M. 1969. Comparative prey-attack studies in newborn snakes of the genus *Thamnophis*. *Behaviour* 33:77–114.
- . 1975. Chemical prey preference polymorphism in newborn garter snakes. *Thamnophis sirtalis*. *Behaviour* 52:202–225.
- . 1977. Learning processes in reptiles. Pp. 555–681. In C. Gans and D. Tinkle (Eds.), *The Biology of the Reptilia*, Vol. 7. Ecology and Behavior. Academic Press, New York.
- . 1978. Behavioral ontogeny in reptiles: Whence, whither, and why? Pp. 149–174. In G. M. Burghardt and M. Bekoff (Eds.), *The Development of Behavior: Comparative and Evolutionary Aspects*. Garland STPM Press, New York.
- . 1992. Prior exposure to prey cues influences chemical prey preferences and prey choice in neonatal garter snakes. *Animal Behaviour* 44:787–789.
- . 1993. The comparative imperative: genetics and ontogeny of chemoreceptive prey responses in natricine snakes. *Brain, Behavior, and Evolution* 41:138–146.
- BURGHARDT, G. M., AND D. DENNY. 1983. Effects of prey movement and prey odor on feeding in garter snakes. *Zeitschrift für Tierpsychologie* 62:329–347.
- BURGHARDT, G. M., AND M. A. KRAUSE. 1999. Plasticity of foraging behavior in garter snakes (*Thamnophis sirtalis*) reared on different diets. *Journal of Comparative Psychology* 113:277–285.
- BURGHARDT, G. M., D. G. LAYNE, AND L. KONIGSBERG. 2000. The genetics of dietary experience in a restricted natural population. *Psychological Science* 11:69–72.
- BURGHARDT, G. M., AND J. M. SCHWARTZ. 1999. Geographic variations on methodological themes in comparative ethology: A natricine snake perspective. Pp. 69–94. In S. A. Foster and J. A. Endler (Eds.), *Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms*. Oxford University Press, Oxford.
- BURGHARDT, G. M., H. C. WILCOXON, AND J. A. CZAPLICKI. 1973. Conditioning in garter snakes: Aversion to palatable prey induced by delayed illness. *Animal Learning and Behavior* 1:317–320.
- CARO, T. M. 1980. Effects of the mother, object play, and adult experience on predation in cats. *Behavioral and Neural Biology* 29:29–51.
- CARPENTER, C. C. 1952. Comparative ecology of the common garter snake (*Thamnophis sirtalis*), the ribbon snake (*Thamnophis s. sauritus*), and Butler's garter snake (*Thamnophis butleri*) in mixed populations. *Ecological Monographs* 22:235–258.
- CROY, M. I., AND R. N. HUGHES. 1991a. The influence of hunger on feeding behaviour and on the acquisition of learned foraging skills by the fifteen-spined stickleback, *Spinachia spinachia* L. *Animal Behaviour* 41:161–171.
- CROY, M. I., AND R. N. HUGHES. 1991b. The role of learning and memory in the feeding behaviour of the fifteen-spined stickleback, *Spinachia spinachia* L. *Animal Behaviour* 41:149–159.
- CUNNINGHAM, P. N., AND R. N. HUGHES. 1984. Learning of predatory skills by shorecrabs, *Carcinus maenas*, feeding on mussels and dogwhelks. *Marine Ecology Progress Series* 16:21–26.
- CUTHILL, I. C., A. KACELNIK, J. R. KREBS, P. HACCOU, AND Y. IWASA. 1990. Starlings exploiting patches: The effect of recent experience on foraging decisions. *Animal Behaviour* 40:635–640.
- DAY, L. B., D. CREWS, AND W. WILCZYNSKI. 1999. Spatial and reversal learning in congeneric lizards with different foraging strategies. *Animal Behaviour* 57:393–407.
- DAY, T., AND J. D. MCPHAIL. 1996. The effect of behavioural and morphological plasticity on foraging efficiency in the threespine stickleback (*Gasterosteus* sp.). *Oecologia* 108:380–388.
- DICKINSON, J. A. 1979. The Effects of Artificial Cover Availability on the Ecology and Movements of a Population of the Garter Snake, *Thamnophis s. sirtalis*. M. S. Thesis, Central Michigan University.
- DRUMMOND, H. 1983. Aquatic foraging in garter snakes: A comparison of specialists and generalists. *Behaviour* 86:1–30.
- EHLINGER, T. J. 1989. Learning and individual vari-

- ation in bluegill foraging: Habitat-specific techniques. *Animal Behaviour* 38:643–658.
- FITCH, H. S. 1965. An ecological study of the garter snake, *Thamnophis sirtalis*. University of Kansas Publications, Museum of Natural History 15:493–564.
- FORD, N. B., AND G. M. BURGHARDT. 1993. Perceptual mechanisms and the behavioral ecology of snakes. Pp. 117–164. In R. A. Siegel and J. T. Collins (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, Inc., New York.
- GILLINGHAM, J. C., J. ROWE, AND M. A. WEINS. 1990. Chemosensory orientation and earthworm location by foraging eastern garter snakes (*Thamnophis sirtalis*). Pp. 522–532. In D. W. MacDonald, D. Muller-Schwarze and S. E. Natynczuk (Eds.), *Chemical Signals in Vertebrates*, Vol. 5. Oxford University Press, Oxford.
- GRAVES, B. M., M. HALPERN, AND J. C. GILLINGHAM. 1993. Effects of vomeronasal deafferentation on home range use in a natural population of eastern garter snakes (*Thamnophis sirtalis*). *Animal Behaviour* 45:307–311.
- GREGORY, P. T., AND K. J. NELSON. 1991. Predation on fish and intersite variation in the diet of common garter snakes, *Thamnophis sirtalis*, on Vancouver Island. *Canadian Journal of Zoology* 69: 988–994.
- GREENWELL, M. G., M. HALL, AND O. J. SEXTON. 1984. Phenotypic basis for a feeding change in an insular population of garter snakes. *Developmental Psychobiology* 17:457–463.
- HALLOY, M., AND G. M. BURGHARDT. 1990. Ontogeny of fish capture and ingestion in four species of garter snakes (*Thamnophis*). *Behaviour* 112:299–318.
- HERZOG, H. A., JR. 1990. Experiential modification of defensive behaviors in garter snakes, *Thamnophis sirtalis*. *Journal of Comparative Psychology* 104:334–339.
- HOLTZMANN, D. A., T. W. HARRIS, G. ARANGUREN, AND E. BOSTOCK. 1999. Spatial learning of an escape task by young corn snakes, *Elaphe guttata guttata*. *Animal Behaviour* 57:51–60.
- HUGHES, R. N., AND C. M. BLIGHT. 1999. Algorithmic behaviour and spatial memory are used by two intertidal fish species to solve the radial maze. *Animal Behaviour* 58:601–613.
- HUGHES, R. N., M. J. KAISER, P. A. MACKNEY, AND K. WARBURTON. 1992. Optimising foraging behaviour through learning. *Journal of Fish Biology* 41: 77–91.
- JAYNE, B. C., AND A. F. BENNETT. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* 44:1204–1229.
- KAMIL, A. C., AND H. L. ROITBLAT. 1985. The ecology of foraging behavior: implications for animal learning and memory. *Annual Review of Psychology* 36:141–169.
- KRAUSE, M. A. 2000. Plasticity of Morphology, Chemosensation, and Predatory Behavior in Garter Snakes (*Thamnophis sirtalis*). Ph.D. Dissertation, University of Tennessee, Knoxville.
- KREBS, J. R., AND A. J. INMAN. 1994. Learning and foraging: Individuals, groups, and populations. Pp. 46–65. In L. A. Real (Ed.), *Behavioral Mechanisms in Evolutionary Ecology*. University of Chicago Press, Chicago.
- LAWTON, P. AND R. N. HUGHES. 1985. Foraging behaviour of the crab *Cancer pagurus* feeding on gastropods *Nucella lapillus* and *Littorina littorea*: Comparison with optimal foraging theory. *Marine Ecology Progress Series* 27:143–154.
- LIND, A. J., AND H. H. WELSH. 1994. Ontogenetic changes in foraging behavior and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*. *Animal Behaviour* 48:1261–1273.
- MACKNEY, P. A., AND R. N. HUGHES. 1995. Foraging behaviour and memory in sticklebacks. *Behaviour* 132:1241–1253.
- MORI, A. 1994. Prey-handling behaviour of newly hatched snakes in two species of the genus *Elaphe* with comparison to adult behaviour. *Ethology* 97: 198–214.
- . 1996. A comparative study of the development of prey-handling behavior in young rat snakes, *Elaphe quadrivirgata* and *E. climacophora*. *Herpetologica* 52:313–322.
- NELSON, K. J., AND P. T. GREGORY. 2000. Activity patterns of garter snakes, *Thamnophis sirtalis*, in relation to weather conditions at a fish hatchery on Vancouver Island, British Columbia. *Journal of Herpetology* 34:32–40.
- POLSKY, R. H. 1975. Developmental factors in mammalian predation. *Behavioral Biology* 15:353–382.
- ROSSMAN, D. A., N. B. FORD, AND R. A. SEIGEL. 1996. *The Garter Snakes: Evolution and Ecology*. University of Oklahoma Press, Norman, Oklahoma.
- SAVITSKY, B. A., AND G. M. BURGHARDT. 2000. Ontogeny of predatory behavior in the aquatic specialist snake, *Nerodia rhombifer*, during the first year of life. *Herpetological Monographs* 14:401–419.
- SHETTLEWORTH, S. J. 1998. *Cognition, Evolution, and Behavior*. Oxford University Press, New York.
- SIH, A. 1993. Effects of ecological interactions on forager diets: Competition, predation risk, parasitism and prey behavior. Pp. 182–211. In R. N. Hughes (Ed.), *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour*. Blackwell Science, Oxford.
- TERRICK, T. D., R. L. MUMME, AND G. M. BURGHARDT. 1995. Aposematic coloration enhances chemosensory recognition of noxious prey in the garter snake *Thamnophis radix*. *Animal Behaviour* 49:857–866.
- VALONE, T. J. 1992. Patch estimation via memory windows and the effects of travel time. *Journal of Theoretical Biology* 157:243–251.
- VARGAS, A., AND S. H. ANDERSON. 1998. Ontogeny of black-footed ferret predatory behavior towards prairie dogs. *Canadian Journal of Zoology* 76:1696–1704.
- YEAGER, C. P., G. M. BURGHARDT, AND L. LYMAN-HENLEY. 1996. Prey handling in three species of garter snakes (*Thamnophis*): Novelty, interference, and facilitation effects. Manuscript in preparation.
- YOERG, S. I. 1994. Development of foraging behaviour in the Eurasian dipper, *Cinclus cinclus*, from fledging until dispersal. *Animal Behaviour* 47:577–588.