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ONTOGENY OF WATER SNAKE FORAGING ECOLOGY¹

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Abstract. Using an index of relative importance we analyzed the stomach contents of over 300 water snakes (*Nerodia* spp.). Ontogenetic changes in prey consumption are most striking in *Nerodia erythrogaster* (number with food in gut = 44) and *N. fasciata* ($N = 72$). Prey of these two species changes from fish to frogs as the snakes exceed a snout–vent length of 50 cm. *Nerodia rhombifera* ($N = 159$) and *N. cyclopion* ($N = 65$) primarily eat fish throughout their life. However, with maturity and increased body size both species change portions of their diets. *Nerodia rhombifera* preys upon larger fish which occupy deeper, open-water habitats, when the snakes exceed 80 cm. *Nerodia cyclopion* eats a larger proportion of centrarchid fish as its body size increases. Small prey are found in the stomachs of most size-classes of all four snake species. Regression analysis indicates that all four species eat larger prey as they mature. However, the largest individuals are females, and in two of the four species the large females eat a different array of prey than smaller conspecific males. The size sexual dimorphism does not reduce the overlap in the diets of the two species that eat anurans as adults.

Key words: foraging ecology; *Nerodia* spp.; ontogeny; predator–prey interactions; Reptilia; sexual dimorphism; water snakes.

INTRODUCTION

In the southeastern United States, water snakes (genus *Nerodia*) are among the most abundant reptiles. The ecological role of this group of predators in the aquatic and semiaquatic systems in which they are found has received some recent attention but remains poorly understood (Mushinsky and Hebrard 1977, Kofron 1978). The local abundance and relative ease of rearing water snakes in the laboratory have facilitated studies of the interactions of genetic and environmental factors that shape reptilian predator–prey systems. Reports on the flexibility of a snake's predisposition for a particular array of prey are numerous (Dix 1968, Burghardt and Pruitt 1975, Gove and Burghardt 1975, Arnold 1978, 1981, Burghardt 1978, 1980, Dunbar 1979, Mushinsky and Lotz 1980). In spite of this effort to quantify and understand the responses of newborn snakes to commonly ingested prey species, a large gap exists in the application of these laboratory findings to field observations (Arnold 1978). Furthermore, most laboratory studies are short term and do not consider possible ontogenetic changes in predator–prey relations. Prey preferences expressed by newborn snakes that weigh 15 g may change considerably by the time an individual matures and weighs 1500 g. Ontogenetic dietary shifts could expand the

variety of resources available to older, and therefore larger, snakes and concurrently decrease predation on prey of smaller stenophagic conspecifics.

Constancy and stability of predator–prey interactions as a predator grows and matures are rarely mentioned in the literature. Two notable exceptions are recent studies by Stoner (1980) and Livingston (1980) that documented five major ontogenetic stages in the diet of pinfish, *Lagodon rhomboides*. Carpenter (1952) and Fitch (1965) recognized that garter snakes (*Thamnophis* spp.) take larger prey as they increase in size, and a recent field study of the striped swamp snake (*Regina alleni*) revealed an ontogenetic change in food habits that reflects an opportunistic use of seasonally abundant prey species (Godley 1980). Shine (1977) analyzed the prey of elapid snakes and concluded that because prey size is small relative to snake size, they are not selective feeders. Vorris and Moffett (1981) reported that the beaked sea snake (*Enhydrina schistosa*) shows some prey (size) discrimination but there was a disproportionately large number of young prey taken by large snakes.

Pough (1978) found that large water snakes can sustain maximum locomotor activity five to eight times longer than newborn snakes. Based upon that finding Pough predicted that larger water snakes should take larger prey (relative to body size), as is the case in garter snakes (Pough 1977). Here we test Pough's prediction, using field data that document ontogenetic patterns in the foraging ecology of four sympatric water

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snake species. In addition, the following questions are posed. If there are ontogenetic shifts in prey consumed by a snake species, are these changes strictly a manifestation of morphological development? Are there corresponding changes in foraging sites and feeding techniques? And finally, does the sex of the predator influence the prey consumed?

MATERIALS AND METHODS

All fieldwork was conducted in a single study area in Ascension Parish, Louisiana, USA, that is part cypress swamp and part bottomland hardwood forest. Snakes included in these analyses were collected between June 1974 and August 1979. About 10% of the gut contents were obtained from snakes that were killed and immediately preserved; the remainder were from snakes that were forced to regurgitate. All prey items were identified, and the mass and volume of each were determined, the latter by water displacement. The contents of 340 snake stomachs were recorded. Those snakes with food in their gut represent 16.7% of our total snake sample. We report on the gut contents of 159 *Nerodia rhombifera*, 72 *N. fasciata*, 65 *N. cyclopion*, and 44 *N. erythrogaster*.

We evaluated ontogenetic patterns in the water snakes diet by pooling feeding data within snake size-classes and calculating an index of relative importance (Pinkas et al. 1971) for each taxon of prey. The index of relative importance (IRI) is:

$$IRI = (\%N + \% Vol) (\%F),$$

where %N = numerical percent of a prey item in the pooled stomachs, % Vol = percent of the volume occupied by that prey item, and %F = number of stomachs that contained that prey. We calculated IRI values at 10-cm increments of snout-vent length for each of the four species. The 10-cm intervals best reflect meaningful ontogenetic trends in foraging and yet are sufficiently sensitive to reveal transition points as they occur in the diet of each snake species.

There are natural groupings of prey above the species level which were chosen to identify ontogenetic patterns. These groups were defined after several permutations of the data suggested that these combinations are biologically significant to these water snakes. All anurans are pooled to form one major prey category, and all fish are combined to form the other major category. Within the fish category we formed several additional prey categories. The large centrarchids (*Lepomis*, *Micropterus*, and *Pomoxis*) are pooled (individuals displaced > 3 mL water), as are all small fish (*Elassoma*, *Fundulus*, *Gambusia*, *Heterandria*, and *Poecilia*). Members of the small-fish category displaced <1 mL water. In some snake species, *Gambusia affinis* was so prevalent that it is treated individually. Finally, we combined the following genera into a category we call large (open-water) fish: *Lepomis*, *Ictalurus*, *Micropterus*, *Dorosoma*, *Cyprinus*,

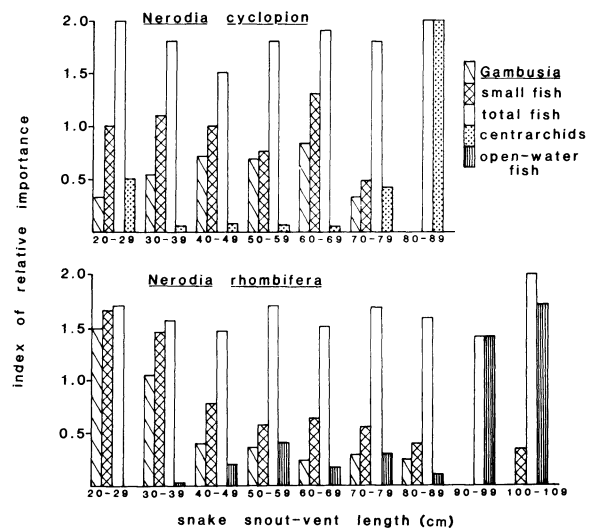


FIG. 1. Ontogenetic profile of the foraging trends of the two fish-eating species of water snakes. The index of relative importance is explained in the text.

Amia, *Anguilla*, and *Pomoxis*; these fish generally are not found within 25 cm of the shore. We separated fish species that are typically in deeper waters because a snake would probably use a different hunting behavior in the deeper water than the side-to-side sweeping behavior commonly used by snakes in shallow water.

A *t* test was used to compare ($P < .01$) the absolute size (volume) of prey taken by small (snout-vent <50 cm) vs. large members of each species of snake. We also used log-transformed data to evaluate the relationship between prey mass and snake mass for each species and for the two sexes within species. The sizes of prey eaten by each sex were compared. Regression slopes and intercepts ($P < .05$) were compared with an analysis of covariance.

RESULTS

The foraging profile of each snake species is unique ontogenetically. Small fish, especially *Gambusia affinis*, are important prey of *Nerodia rhombifera* until the snakes attain a snout-vent length >80 cm. Large fish, such as shad (*Dorosoma*) and catfish (*Ictalurus*), become a major component in the diets of very large members of this species. The other fish-eating snake, *N. cyclopion*, also preys heavily upon small fish until it reaches a length of ≈ 70 cm. Large individuals eat sunfish (*Lepomis*) and bass (*Micropterus*; Fig. 1, Table 1).

Although some young *Nerodia fasciata* occasionally eat anurans, frogs are not an important prey until the snakes exceed 50 cm. Snakes less than that size are primarily piscivorous. The ontogenetic profile of *N. erythrogaster* illustrates an abrupt and virtually complete shift from fish to anurans as the snake exceeds 50 cm in snout-vent length (Fig. 2, Table 1).

TABLE 1. The number, volume, and frequency (number of stomachs containing each prey) for the four most prevalent prey categories for each species of water snakes. For each prey species, data are partitioned into 10-cm increments of snake snout-vent length. The categories are defined in the text.

Snake		<i>Gambusia</i>			Small fish			Total fish			Other		
S-V length (cm)	Sample size	N	Vol. (mL)	Freq.	N	Vol. (mL)	Freq.	N	Vol. (mL)	Freq.	N	Vol. (mL)	Freq.
<i>Nerodia fasciata</i>													
20-29.9	7	27	5.6	.71	45	8.5	.86	45	8.5	.86	2	6.0	.29
30-39.9	11	14	3.2	.64	39	10.9	.64	41	25.9	.82	4	11.0	.27
40-49.9	8	28	5.4	.63	34	7.2	.75	39	19.7	.88	1	2.0	.13
50-59.9	20	27	9.9	.60	60	14.8	.60	63	16.0	.65	8	52.5	.40
60-69.9	14	15	5.3	.36	42	10.8	.43	53	54.3	.57	8	59.7	.43
70-79.9	11	1	0.5	.09	3	0.7	.18	4	52.7	.27	9	76.5	.82
80-89.9	1	1	0.1	1.0	1	0.1	1.0	1	0.1	1.0	1	5.0	1.0
20-49.9	26	69	14.2	.65	118	26.6	.73	125	54.2	.85	7	19.0	.23
50-89.9	49	44	15.8	.41	106	26.4	.46	121	123.0	.54	26	193.7	.52
<i>Nerodia erythrogaster</i>													
20-29.9	2	2	0.5	.5	7	1.2	.5	8	4.7	1.0	0	0	...
30-39.9	6	3	0.2	.17	8	0.9	.5	9	3.1	.67	2	14.0	.33
40-49.9	8	62	13.1	.75	76	20.3	.75	77	21.3	.88	4	9.5	.38
50-59.9	8	15	7.0	.25	30	14.5	.38	30	14.5	.38	18	58.5	.88
60-69.9	1	0	0	...	0	0	...	0	0	...	1	35.0	1.0
70-79.9	3	0	0	...	0	0	...	0	0	...	7	32.0	1.0
80-89.9	7	1	0.5	.14	2	0.8	.14	4	20.8	.29	8	76.0	.86
90-99.9	5	0	0	...	0	0	...	0	0	...	10	127.5	1.0
100-109.9	4	5	2.3	.25	5	2.3	.25	8	60.8	.50	2	292.0	.50
20-49.9	16	67	13.8	.47	91	22.4	.59	94	29.1	.76	6	23.5	.35
50-109.9	28	21	9.8	.14	37	17.6	.18	42	96.1	.25	46	621.0	.86
<i>Nerodia cyclopion</i>													
20-29.9	2	1	1	.5	2	1.1	.5	3	3.0	1.0	1	2.0	.5
30-39.9	6	13	3.7	.67	21	7.7	.83	24	11.7	1.0	1	2.0	.17
40-49.9	7	29	4.9	.71	33	7.9	.86	36	17.9	.86	2	9.0	.14
50-59.9	13	39	13.3	.69	43	13.8	.69	46	73.0	.92	1	44.0	.08
60-69.9	17	93	34.6	.65	112	42.5	.82	117	65.5	1.0	3	19.5	.18
70-79.9	17	29	13.0	.65	39	17.7	.71	62	165.2	.94	21	119.5	.41
80-89.9	3	0	0	...	0	0	...	3	156.0	1.0	3	156.0	1.0
20-49.9	15	43	9.6	.67	56	16.7	.87	63	32.7	.93	4	13.0	.20
50-89.9	50	161	60.9	.64	194	73.9	.70	228	459.7	.96	28	339	.27
<i>Nerodia rhombifera</i>													
20-29.9	4	58	4.0	1.0	64	4.5	1.0	66	4.6	1.0	0	0	...
30-39.9	13	79	16.1	.85	97	21.9	.92	100	24.6	.93	2	2.4	.15
40-49.9	37	126	29.7	.59	214	67.2	.62	228	138	.86	12	69.7	.42
50-59.9	36	100	26.2	.47	121	38.2	.58	147	150.4	.94	31	95.3	.36
60-69.9	30	72	25.3	.37	117	39.1	.60	136	139.3	.83	22	36.0	.24
70-79.9	18	45	12.5	.50	68	20.3	.61	89	94.9	.94	16	49.1	.34
80-89.9	10	13	8.3	.50	21	14.5	.50	28	11.5	.90	8	78.5	.30
90-99.9	8	0	0	...	0	0	...	6	750.0	.75	6	750	.75
100-109.9	3	0	0	...	1	1.0	.33	3	373.0	1.0	2	372	.67
20-49.9	54	263	49.8	.69	375	93.6	.72	394	167.2	.89	14	72.1	.32
50-109.9	104	230	72.3	.40	327	112.5	.53	408	1597	.89	85	1381	.55

The results of the comparisons of the mean volume of each prey item found in the two size-classes of snakes are shown in Table 2. Snakes <50 cm eat prey that average ≈ 0.5 mL in volume. Large members of all four species eat significantly larger prey than do smaller conspecifics. Among these large snakes the relationship between predator size and prey size is noteworthy. The mean volume of prey size forms a hierarchy that parallels snake size. An average prey item ingested by *N. rhombifera* is significantly larger ($P < .01$) than prey of the other fish-eating species,

N. cyclopion. The same is true of prey of the larger *N. erythrogaster* when compared to prey of *N. fasciata*.

The regression of log prey mass on log snake mass is presented in Figs. 3 and 4. The only regression not significant with $P < .01$ is that of *Nerodia fasciata* males ($F = 3.4$, $P = .045$). The analysis of covariance comparing the regression slopes between the sexes of each species yielded significant ($P > .05$) differences between *Nerodia rhombifera* and *N. cyclopion* males and females. In *Nerodia rhombifera* the intercepts are

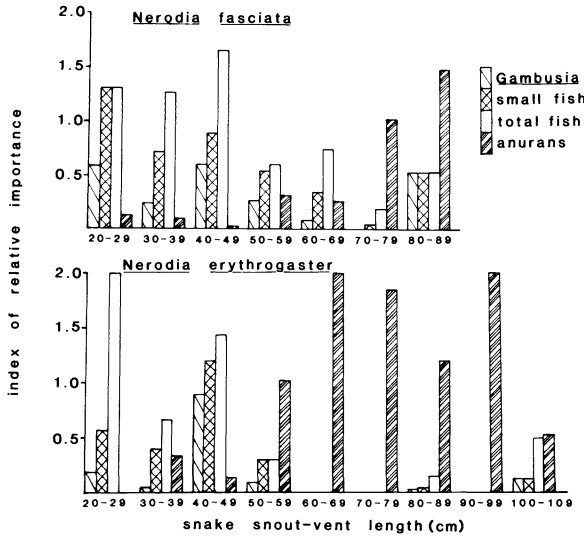


FIG. 2. Ontogenetic profile of the foraging trends of the two anuran-eating species of water snakes.

also significantly different between males and females. There are no significant differences in slopes or intercepts of the regression lines for males and females of *N. fasciata* or *N. erythrogaster*.

DISCUSSION

The data clearly indicate ontogenetic changes in the diets of all four water snake species. The prey most frequently ingested by each snake species include several species of small fish and one or two larger prey. It is in these larger prey species that we found distinct differences within and among snake species. *Gambusia* and *Heterandria* are among the relatively most important prey of all four snakes, and all individuals <50 cm in snout-vent length eat these very small prey. Each of the four snake species eats significantly larger prey as the snake body size increases. The largest snake, *Nerodia erythrogaster*, was found to eat the largest prey. The other anuran-eating snake, *N. fasciata*, is the smallest of the four snakes and eats prey with a mean volume ≈25% that of *N. erythrogaster* prey. Large individuals of the two fish-eating species have similar mean body sizes, but *N. rhombifera* eats larger prey than does *N. cyclopion*. It is noteworthy that most size-classes of all four species do ingest very small prey.

Knowing that large snakes eat prey not ingested by smaller conspecifics enables us to make inferences about changes in foraging sites and behaviors. We have observed all sizes of the four species feeding frequently in very shallow water. These snakes make sweeping side-to-side, figure-eight patterns with their mouths open, and will often use their bodies to entrap small fish. Drummond (1979) experimentally demonstrated that visual, chemical, and tactile stimuli are all impor-

TABLE 2. Average volume of each prey item consumed by different size-classes of water snakes. A *t* test for difference between the average volume of prey items taken by the two size-classes of snakes was significant at *P* < .01 for each of the four species.

Species	N	Snake size-class (S-V) (cm)	Mean size of snakes (cm)	Mean volume of prey (mL)
<i>Nerodia rhombifera</i>	54	20-49.9	41.5	0.50
	104	50-110	67.8	3.84
<i>Nerodia cyclopion</i>	15	20-49.9	39.8	0.57
	50	50-100	65.6	2.02
<i>Nerodia fasciata</i>	26	20-49.9	35.8	0.55
	46	50-100	63.4	1.90
<i>Nerodia erythrogaster</i>	16	20-49.9	39.3	0.56
	28	50-111	78.6	7.89

tant when a water snake is using this feeding technique. The large prey of *Nerodia rhombifera* and *N. cyclopion* are found in deep waters where the snakes would be forced to use a different feeding technique. Our work during the warm months, when feeding is most frequent, was mostly at night in opaque water that prevented any direct observations of deep-water foraging. Likewise, the two anuran-eating snake species would also change foraging techniques as they switch from eating small fish to anurans. Both frogs and toads are abundant along the shoreline of the bayous, so the actual site of feeding may not change as dramatically as the prey species consumed.

Females of all four species are larger than conspecific males. Fitch (1981) found this to be the case for most members of the entire subfamily (Natricinae) and reported a female to male size ratio of 124% for members of the genus *Nerodia*. An interesting dichotomy in the ecological effects of this sexual dimorphism is exhibited by the species studied here. The analyses of covariance of the regression of prey mass on snake mass indicate that sexual dimorphism affects the diet in the two fish-eating species but not the two anuran-eating species. Large females of the fish-eating snakes eat larger prey than do conspecific males. However in the two species that eat anurans as adults, the typical size of the prey is such that large females as well as the somewhat smaller males can both ingest the same prey. Fitch (1981) stated that sexual dimorphism in reptiles is often viewed as a means of relieving intraspecific competition by partitioning available food resources. He also recognized that in species with large females, reproductive success is promoted by the fact that females as well as males are relieved from competition by immatures. Our data confound these two empirically accurate statements. In the two species that eat anurans as adults, the size of the prey is such that the diets of the two sexes overlap.

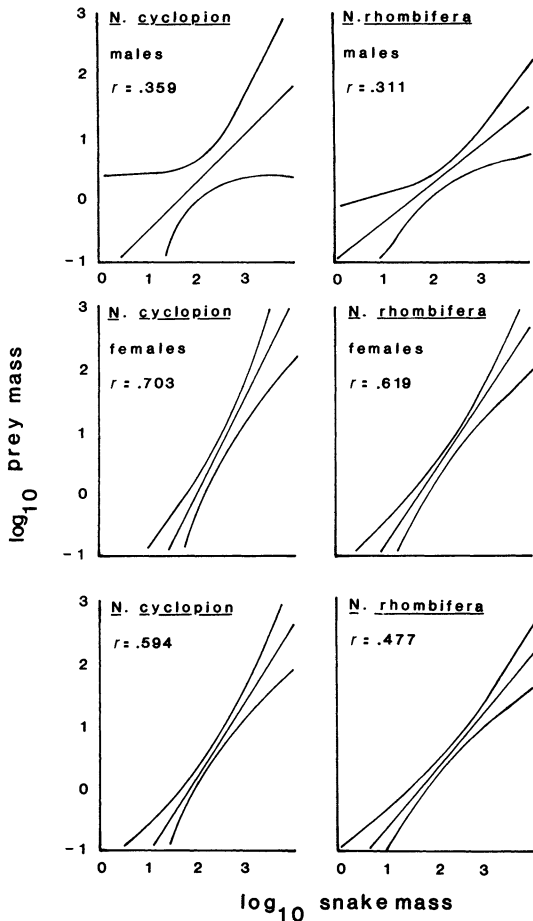


FIG. 3. A plot of the relationship between log of prey mass and log snake mass for the two species that eat fish throughout their life history. The sexes are presented both separately and combined. The 95% confidence limits are represented.

Why do these two species switch to anurans? Experimental work on newborn of the two anuran-eating water snakes has shown an ontogenetic tendency to switch from fish to anuran prey, regardless of prior feeding experience, by *Nerodia erythrogaster*. Maturing *N. fasciata* also responded with increasing intensity toward anurans, but the responses were more variable than those of *N. erythrogaster* (Mushinsky and Lotz 1980). We can speculate that through evolutionary time natural selection sufficiently favored those who made the switch to anurans so as to fix a genetic component to prey selection. This strongly suggests that anurans (especially *Bufo* spp.) are an abundant and predictable food resource for these populations of snakes.

Our findings indicate, as do those of Stoner (1980), Livingston (1980), and Godley (1980), that the species is not necessarily the ecological functional unit, as is often assumed in contemporary ecological theory. In

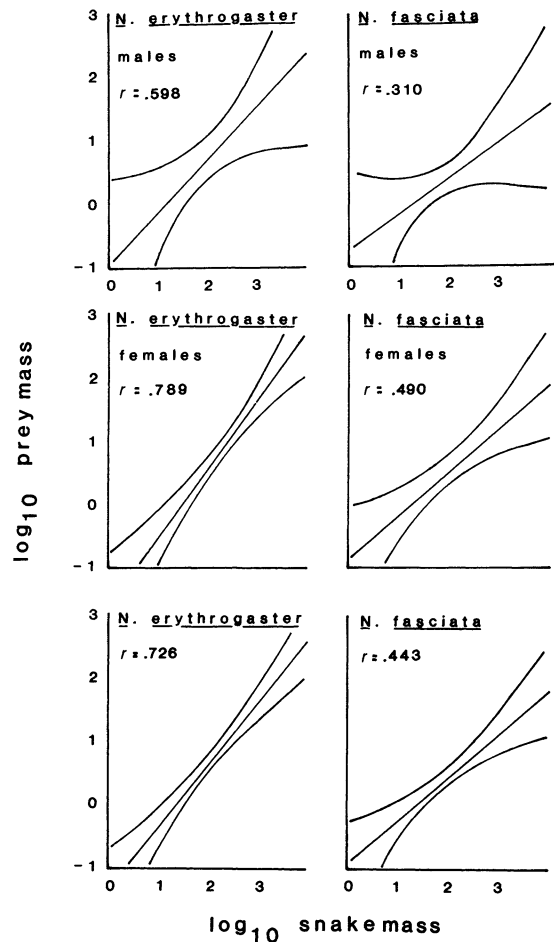


FIG. 4. A plot of the relationship between log prey mass and log snake mass for the two species that ingest anurans as adults. The sexes are presented both separately and combined. The 95% confidence limits are represented.

fact, all four snake species can be considered a single trophic unit (Livingston 1980) until a certain body size is attained, and thereafter each functions as a separate feeding unit. The documentation of ontogenetic shifts in diet should also serve to caution those who place confidence in the results of short-term feeding and rearing experiments in the laboratory. (See Burghardt [1969] for additional cautionary statements regarding laboratory studies of snake feeding.) The responses of young snakes in the field seem to be governed more by prey size and apparent availability rather than a preference per se, and only after the snakes have survived for several years do we see patterns that we can consider characteristic of a species.

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