

Feeding Ecology of the Concho Water Snake, *Nerodia harteri paucimaculata*

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ABSTRACT.—The diet of the Concho water snake *Nerodia harteri paucimaculata* was investigated from 1987 to 1990 by palpation of stomach contents. Prey remains representing 304 prey items were recovered from 192 individual snakes. Concho water snakes were almost completely piscivorous, feeding on 19 species of fish from nine families with minnows (Cyprinidae) dominating numerically. Cricket frogs (*Acris crepitans*) represented the only non-piscine prey. Diet diversity increased ontogenetically according to snake body size. Observations of foraging snakes suggest an ontogenetic change in foraging sites concurrent with a change in diet composition. Prey size was positively correlated with snake body size although some snakes occasionally ingested numerous small prey, possibly due to opportunistic feeding on small prey aggregations. Snakes occasionally attempted to handle prey too large to be ingested. Feeding occurred from mid-March to early November. Gravid females fed throughout the spring into mid-July and resumed feeding after parturition. Neonate and juvenile riverine snakes ingested prey in proportion to apparent availability while adults consumed a disproportionate amount of larger prey species. Lacustrine snakes primarily consumed prey associated with benthic or shallow water habitats. However, few individuals of open water and top water species were ingested, suggesting that prey habitat preference strongly influences catchability in lake systems.

Trophic relationships pervasively influence snake biology. The radiation of morphological and ecological specializations in advanced snakes may have resulted primarily from adaptations to dietary demands (Greene, 1983; Pough and Groves, 1983). Food resources affect the amount of energy allocated to reproduction in female snakes (Seigel and Ford, 1987) and food availability may significantly influence growth in reptiles (Andrews, 1982). Detailed analyses of foraging ontogeny, predator-prey size relationships, and prey selection are needed to enhance the understanding of trophic relationships within snake populations (Mushinsky, 1987).

Harter's water snake (*Nerodia harteri*) is endemic to Texas and is represented by two subspecies, the Concho water snake (*N. h. paucimaculata*) and the Brazos water snake (*N. h. harteri*). Each subspecies occupies a somewhat restricted distribution delimited by the availability of riffle habitat, which provides essential foraging areas and cover for juvenile snakes. The Concho water snake is currently restricted to 396 km of habitat along the upper reaches of the Colorado and Concho river drainages and 25 km of shoreline of three recently created man-made lakes in central Texas (Scott et al.,

1989). This subspecies is currently listed as endangered by the state of Texas and threatened by the U.S. Fish and Wildlife Service.

Although the diets of most North American water snakes are well known, few data exist for the Concho water snake (*N. h. paucimaculata*). Lists of prey items were provided by Williams (1969) and Rose (1989) from 32 and 18 snakes, respectively. Both studies demonstrated a piscivorous diet dominated by minnows. However, these studies only provided taxonomic identities of prey and made no distinctions of snake sex or size.

This study describes the diet and feeding ecology of *N. h. paucimaculata* in central Texas. The major objectives are: (1) To quantitatively describe diet composition. (2) To examine the relationship of prey size to snake body size. We expected differential prey utilization by different sized snakes given the frequency of positive predator-prey size correlations and ontogenetic diet shifts in snakes (Mushinsky, 1987), including other *Nerodia* (Mushinsky et al., 1982; Plummer and Goy, 1984; Miller and Mushinsky, 1990). (3) To compare diet composition with prey availability. Estimates of types and quantities of accessible prey are requisite to any evaluation of prey selection. We use samples of potential prey, collected in snake foraging habitat, to evaluate their apparent availability. (4) To compare the diets of snakes in riverine and lacustrine systems. We examined the diets of lacus-

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trine snakes to evaluate prey utilization in a system artificial to the snake, providing information of potential conservation importance.

MATERIALS AND METHODS

Study areas were located in the Concho valley of central Texas (31°N, 99°W) along the Colorado and Concho rivers and at Lake Moonen, an inundated tributary of the Colorado River. The region undergoes warm, dry summers and mild winters with an average annual temperature of 9.3 C. The frost-free period averages 232 d, from late March to mid-November. The mean maximum and minimum daily temperatures for January are 16 C and 0.6 C, respectively, with corresponding July temperatures of 36 C and 21 C. Annual precipitation averages 45–60 cm, mostly occurring in May and September (Griffiths and Bryan, 1987).

The diet of *N. h. paucimaculata* was investigated over three years (1987–1990) as part of a mark-recapture study. Because we wanted to avoid potential reduction of growth and survivorship of small snakes, collection of neonate prey was discontinued after 1988. Snakes were caught by hand, palpated, and their stomach contents preserved in 10% formalin for later identification. Prey items from gravid or recently post parturient females were identified, measured and gently palpated back into the stomach to minimize effects on survivorship. Snout-vent length (SVL), tail length, mass (excluding prey), and sex also were recorded for each captured snake.

Snakes containing prey items were assigned to one of the following four SVL size categories: neonate—<300 mm; juvenile—300 mm to sexual maturity; adult male—at least 380 mm; adult female—at least 460 mm. Some snakes observed feeding but not captured could reliably be assigned to one of these classes by visual estimation. Minimum size at sexual maturity for each sex was determined by the presence of sperm in the cloacal fluid of males and presence of cloacal sperm or minimum size of gravid individuals in females (Fitch, 1987). The Shannon diversity index, H' , was computed to compare diet specialization between life history categories (Schoener, 1968; Wallace and Diller, 1990). This index was chosen to quantify diet diversity because it is amenable to standard statistical tests for differences among means (e.g., Hutcheson, 1970). The formula used was $H' = -\sum P_i \log_{10} P_i$ where P_i is the proportion of species i in the total sample. When expressed in this form H' may vary from 0 to 1, representing maximum and minimum specialization, respectively. Differences among diversity indices for each size category were compared by two-tailed Student's t -tests using the method of Hutcheson

(1970). Alpha levels were adjusted to 0.01 to ensure an overall protection level of 0.05 (Zar, 1984).

Diet overlap between snake life history categories was estimated using the symmetric index of Pianka (1986):

$$O_{jk} = \frac{\sum P_{ij} P_{ik}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}}$$

where P_{ij} and P_{ik} represent the proportion of prey item i in the diet of snake categories j and k , respectively. This formula provides values ranging from 0 (no overlap) to 1 (complete overlap). This overlap measure has been used previously to quantify dietary similarity in snake studies (e.g., Gregory, 1978; Brown and Parker, 1982; Henderson, 1982; Gregory, 1984), it is intended here only as a descriptive measure of dietary concordance among population subsets.

Kendall's Tau, a nonparametric measure of correlation, was utilized to determine the relationship between predator size and prey size using snake SVL and total length of prey. Because some snakes (20%) contained multiple prey, separate correlations were calculated for stomachs containing individual prey, the largest individual item in each multiple prey sample, and both combined. Total length, mass, and three size index measurements (head length, caudal peduncle width, and dorsal fin to tail length) were measured for a series of 30 to 50 whole individuals of nine seine-sampled prey species. For the prey genus *Pimephales*, body measurements from the most common prey species, *vigilax*, also were used to estimate the very similar *promelas*. Each index measurement was then regressed against total length and mass to generate equations which were implemented to predict the original size and weight of partially digested prey items (Voris and Moffett, 1981). All body measurements were strong predictors ($R^2 = 0.95$ – 0.99) of total length and mass for all prey species.

Samples of prey species were collected twice yearly with a three meter seine in available foraging habitat at several study areas within the Concho and Colorado river drainages and at Lake Moonen. Seines were drawn upstream through riffles, at riverine sites, or parallel to shore for at least 20 m in lake habitat. Lake prey sampling was limited to the area within three meters of shore because steep shoreline gradients produced water depths considerably greater than seine height further away. We suggest that water depths outside this shoreline margin also could preclude foraging attempts by these relatively small snakes which forage naturally in shallow riffles (Scott et al., 1989). All captured fishes small enough for snakes to swallow, judged by the range of prey sizes found in snake

stomachs, were preserved in 10% formalin and later identified and counted in the laboratory.

Seining may have deficiencies as a sampling technique for evaluating prey availability. The assumption that all seine-sampled fish are available to snakes is very subjective. Seines also undoubtedly do not sample all fish sizes with equal efficiency. We also speculated that certain secretive fish species, such as darters and catfish, might be underrepresented by seining. However, samples obtained by electroshocking were similar in composition and relative abundance. Despite these potential problems we feel that seine samples provided a credible estimate of apparent prey availability. Seines collected all prey commonly ingested by snakes representing the entire range of prey sizes found in snake stomachs.

Differences in the expected ingestion of prey by snakes, compared with snake diet, were assessed using a χ^2 test of homogeneity among diet and seine samples. The utilization of individual prey types was evaluated by comparing individual expected values from the χ^2 calculations with actual usage estimated by simultaneous Bonferroni confidence intervals (Neu et al., 1974; Byers and Steinhorst, 1984). These are conservative intervals which bound the probability error rate by scaling the significance level according to the number of resource categories compared. Prey categories were considered to be consumed out of proportion to availability if the expected proportion of usage was not bounded by the interval. Prey species were grouped taxonomically by family to facilitate analysis. The fish species *Aplodinotus grunniens* and *Cyprinodon rubrofluvialis*, each represented once in the diet sample but not recorded in seine samples, and *Moxostoma congestum*, represented by four seine-sampled specimens but absent from diet samples, were excluded from availability analyses. A significance level of 0.05 was used throughout except where otherwise stated.

RESULTS

The handling of over 6000 Concho water snakes during 1987-1990 yielded 258 prey items from 191 individual *N. h. paucimaculata*. Each snake represented was sampled only once. Concho water snakes were almost exclusively piscivorous and fed on 20 prey species. Sixteen prey species were recorded for riverine snakes (Table 1) for which minnows (Cyprinidae) dominated the diet, accounting for 79% of all recorded prey items. Neonates fed almost entirely on minnows, represented mostly by the red shiner (*Notropis lutrensis*) and were the only size category found to consume cricket frogs (*Acris crepitans*). Juveniles and adult males consumed

mostly minnows but also ate catfish (*Ictalurus punctatus* and *Pylodictus olivaris*). Adult females fed mainly on the larger prey species, including catfish, sunfish (*Lepomis* sp.), and gizzard shad (*Dorosoma cepedianum*), and displayed the greatest dietary diversity by consuming 13 of the 16 prey species recorded. Riverine fish taxa sampled from pool habitats (e.g., bass *Micropterus* sp., crappie *Pomoxis* sp., and black bullheads *Ictalurus melas*) were not observed in the diet of *N. h. paucimaculata*, suggesting that foraging activity is confined to riffles.

The Shannon diversity indices for each size category of riverine snakes varied from 0.45 for neonates to 0.94 for adult females. All riverine snakes combined provided an index value of 0.73. The Shannon index value for neonates was not significantly different from juveniles ($t = 1.69$, $df = 155$, $P > 0.09$) or adult males ($t = 1.75$, $df = 115$, $P > 0.05$) but differed significantly from adult females ($t = 7.38$, $df = 132$, $P < 0.001$). A significant difference occurred in this index between juveniles and adult females ($t = 6.30$, $df = 109$, $P < 0.001$) but not between juveniles and adult males ($t = 0.50$, $df = 98$, $P > 0.5$). There was a significant difference in the index between adults of each sex ($t = 4.15$, $df = 81$, $P < 0.001$).

Diet composition among size categories was similar as evidenced by high overlap values (neonate-juvenile: 0.996; neonate-adult male: 0.999; neonate-adult female: 0.788; juvenile-adult male: 0.997; juvenile-adult female: 0.835; adult male-adult female: 0.869). The dietary similarity of neonates, juveniles, and adult males results from the numerical dominance of minnows in the diets of these groups. The greatest change in diet occurred in adult females where prey diversity increased with a corresponding decrease in minnow consumption.

All size categories of riverine Concho water snakes ingested some prey with greater frequency than expected based on prey availability estimates collected from seine samples. The relative abundances of prey species sampled in each river drainage were similar ($\chi^2 = 4.66$, $df = 4$, $P > 0.25$) and these data were pooled for subsequent analyses. Neonates, in general, ingested prey in proportion to abundance ($\chi^2 = 0.33$, $df = 3$, $P > 0.25$) (Table 2). The diet of juvenile snakes differed significantly from the prey available ($\chi^2 = 19.77$, $df = 3$, $P < 0.001$). These snakes ingested more ictalurid prey than expected while ingesting minnows and centrarchids in proportion to availability. Adult males also selected ictalurids ($\chi^2 = 31.16$, $df = 4$, $P < 0.001$) while ingesting minnows, poeciliids, centrarchids, and sciaenids in proportion to availability. Adult females showed a preference for larger prey including ictalurids,

TABLE 1. Prey of riverine Concho water snakes sampled during 1987-1990. n = number of stomachs; N = total number of prey items; M = total mass of prey; % = % occurrence in individual stomachs containing prey. Based on 258 prey items from 143 snakes. H' = Shannon diversity index.

Prey	Neonates (n = 58)			Juveniles (n = 30)			Adult male (n = 19)			Adult female (n = 31)			Total* (n = 143)		
	N	M	%	N	M	%	N	M	%	N	M	%	N	M	%
Cyprinidae															
<i>Notropis lutrensis</i>	61	33.2	63.8	23	16.3	36.6	33	21.0	31.6	9	8.9	19.4	127	80.7	42.7
<i>Pimephales vigilax</i>	16	15.4	24.1	29	18.2	36.6	9	5.9	26.3	7	10.8	19.4	61	52.1	25.9
<i>P. promelas</i>	3	2.9	5.2	5	8.2	13.3	—	—	—	—	—	—	8	11.1	4.9
<i>Cyprinus carpio</i>	—	—	—	1	3.8	3.3	—	—	—	3	6.9	3.2	5	14.1	2.1
Ictaluridae															
<i>Ictalurus punctatus</i>	1	1.0	1.7	1	3.5	3.3	1	—**	5.3	7	95.4**	22.6	10	99.9**	7.0
<i>Pylodictus olivaris</i>	—	—	—	5	17.7	16.6	4	19.9	21.1	6	113.9**	19.4	17	151.5**	11.9
Poeciliidae															
<i>Gambusia affinis</i>	3	1.5	5.2	—	—	—	2	0.8	5.3	1	0.7	3.2	6	3.0	3.5
Centrarchidae															
<i>Lepomis cyanellus</i>	—	—	—	—	—	—	—	—	—	4	177.7	12.9	4	177.7	2.8
<i>L. macrochirus</i>	1	0.4	1.7	—	—	—	2	0.8	5.3	1	0.4	3.2	4	1.6	2.1
<i>L. megalotis</i>	—	—	—	—	—	—	—	—	—	1	23.5	3.2	1	23.5	0.7
<i>Lepomis</i> sp.	—	—	—	—	—	—	1	2.2	5.3	1	—	3.2	3	2.2	2.1
<i>Micropterus punctulatus</i>	—	—	—	1	3.6	3.3	—	—	—	—	—	—	1	3.6	0.7
Percidae															
<i>Etheostoma spectabile</i>	2	1.3	3.4	—	—	—	—	—	—	—	—	—	2	3.4	1.4
Sciaenidae															
<i>Aplodinotus grunniens</i>	—	—	—	—	—	—	1	11.0	5.3	—	—	—	1	11.0	0.7
Cyprinodontidae															
<i>C. rubrofluvialis</i>	1	1.0	1.7	—	—	—	1	1.4	5.3	—	—	—	2	2.4	1.4
Clupeidae															
<i>Dorosoma cepedianum</i>	—	—	—	—	—	—	1	3.7	5.3	4	34.5**	12.9	5	38.2	3.5
Anura															
<i>Acris crepitans</i>	1	0.5	1.7	—	—	—	—	—	—	—	—	—	1	0.5	0.7
Totals	89	54.6		65	63.0		55	68.7		44	478.9		258	673.2	
Shannon index		0.45			0.56			0.61			0.94			0.73	

* Includes five prey items from snakes of unknown life history categories.

** Some prey items in these categories recorded as field observations; masses were not obtained.

TABLE 2. Number and percent frequency of prey types in the diet of life history categories of riverine Concho water snakes as compared to prey availability. N = number of prey items; % = percent of total number. Based on 253 prey items from 138 snakes.

Prey type	Percent frequency									
	Prey sampled		Neonates		Juveniles		Adult males		Adult females	
	N	%	N	%	N	%	N	%	N	%
Cyprinidae (Minnows)	12,909	92.1	80	89.9	58	88.2	42	76.4	19	43.2*
Ictaluridae (Catfish)	40	0.3	1	1.1	6	8.8*	5	9.1*	13	29.5*
Poeciliidae (Mosquitofish)	607	4.3	3	3.4	—	—	2	3.6	1	2.3
Centrarchidae (Sunfish)	218	1.6	1	1.1	1	2.9	3	5.5	7	15.9*
Clupeidae (Shad)	41	0.3	—	—	—	—	1	1.8	4	9.1*
Total	—	—	89**	97.6	65	100.0	55**	96.2	44	100.0

* Indicates prey types ingested in different proportion than available at $P < 0.05$ level of significance.

** Total includes prey species not represented by these prey types.

centrarchids, and sciaenids while taking fewer minnows than predicted from apparent availability ($\chi^2 = 615.6$, $df = 4$, $P < 0.001$).

The diet of 48 Concho water snakes from Lake Moonen consisted of eight prey species, including three not recorded in the diet of riverine snakes (Table 3). Prey items from all snake size categories were pooled due to small sample sizes. The dominant prey species in number and biomass was bigscale logperch (*Percina macrolepidida*) which accounted for 35.4% of all prey consumed. The remainder of the diet was comprised mostly of cyprinids (31.2%) and cyprinodontids (20.8%). The Shannon diversity index for Lake Moonen snakes was 0.65.

Lacustrine snakes consumed prey out of proportion to apparent availability ($\chi^2 = 151.81$, $df = 5$, $P < 0.001$). The only prey type consumed in greater numbers than expected was *P. macrolepidida*. The most abundant potential prey, centrarchids and atherinids, were ingested significantly less than expected. All other prey types were consumed in proportion to their apparent availability.

There was a significant positive correlation between length of prey items and snake SVL (Fig. 1). This was true for all calculation methods; stomachs with individual prey (Kendall's Tau = 0.59, $P < 0.001$, $N = 104$), largest item in stomachs with multiple prey (Kendall's Tau = 0.43, $P < 0.001$, $N = 33$), and both conditions combined (Kendall's Tau = 0.46, $P < 0.001$, $N = 137$). Stomach contents were usually represented by a single prey item but multiple prey (2-21 items) were present in 33 (23.1%) of 143 stomachs. Snakes of most size classes occasionally ingested very small prey. Instances of utilization of small prey by large snakes were usually associated with the ingestion of multiple

prey items. On two occasions juvenile snakes were observed to handle fish too large to be ingested.

Snakes were observed to use two different tactics while foraging. Adult snakes were frequently observed actively foraging within riffles which involved random exploratory movements with frequent pauses to examine cavities beneath rocks. Snakes were also observed motionless on immovable objects, while completely or partially submerged, in close proximity to schools of minnows which elicited attacks by snakes as they approached. This behavior was most frequently exhibited by juveniles. All observations of foraging or feeding snakes were associated with riffles, although juveniles tended to forage in shallow riffle margins while adults mainly searched deeper central regions of riffles. The open mouthed searching behavior reported previously for other *Nerodia* (Gillingham and Rush, 1974; Mushinsky and Hebrard, 1977; Drummond, 1979) was never observed.

Analyses of seasonal feeding frequency were not attempted because sampling effort was not uniform and snake catchability varied greatly among seasons. However, the extreme dates recorded for feeding activity were 13 March and 2 November. Gravid females were observed feeding throughout the spring until mid-June and continued foraging into July. Captive gravid females continued to feed until one to two weeks prior to parturition. Post partum females fed from August to early October. Neonates began feeding shortly after birth in August and typically ceased to feed by early October.

DISCUSSION

Our findings of the diet of *N. h. paucimaculata* confirm previous observations of complete pi-

TABLE 3. Diet composition of 48 Lake Moonen Concho water snakes as compared to availability of potential prey species. Diet sample includes 36 neonates and 12 juveniles. Each snake contained one prey item. N, M, and % as in Table 1.

Prey species	Diet			Prey sampled	
	N	M	%	N	%
Cyprinidae					
<i>Notropis lutrensis</i>	5	6.6	10.4	12	1.5
<i>Pimephales vigilax</i>	10	15.9	20.8	86	10.9
Percidae					
<i>Percina macrolepidia</i>	17	42.3	35.4	26	3.3
Centrarchidae					
<i>Lepomis macrochirus</i>	1	0.4	2.1	227	28.9
<i>Micropterus</i> spp.	—	—	—	—	—
Ictaluridae					
<i>Ictalurus melas</i>	1	0.6	2.1	—	—
<i>Ictalurus punctatus</i>	—	—	—	5	0.6
Cyprinodontidae					
<i>Cyprinodon variegatus</i>	10	6.5	20.8	67	8.5
Atherinidae					
<i>Menidia beryllina</i>	3	1.8	6.3	218	27.8
Poeciliidae					
<i>Gambusia affinis</i>	—	—	—	67	8.5
Sciaenidae					
<i>Dorosoma cepedianum</i>	—	—	—	12	1.5
Anura					
<i>Acris crepitans</i>	1	1.0	2.1	—	—
Total	48			784	
Shannon index		0.65			

scivory with substantial consumption of minnows. Williams (1969) reported that three minnow species (*Notropis lutrensis*, *Hybopsis aestivalis*, and *Hybognathus placita*) composed 79% of the prey items recovered from 32 *N. h. paucimaculata* at a site on the upper Colorado River. The remaining prey species included Rio Grande killifish *Fundulus zebrinus* (18%) and channel catfish *Ictalurus punctatus* (3%). Similarly, Rose (1989) found that minnows (*Notropis* sp. and *Hybopsis aestivalis*) accounted for 93% of the prey items recovered from 18 *N. h. paucimaculata*. He also noted that captive specimens consumed minnows but also accepted tadpoles (*Rana blairi*), cricket frogs (*Acris crepitans*), and hellgrammites. Although the latter two organisms were syntopic with *N. h. paucimaculata* at our study sites, we observed only rare ingestion of frogs (*A. crepitans*) under natural conditions.

Investigations of water snake diets have revealed ontogenetic changes in prey utilization to be a consistent ecological trend. Mushinsky et al. (1982) reported distinct ontogenetic dietary shifts in each of four *Nerodia* species in southern Louisiana; *Nerodia erythrogaster* and *N.*

fasciata switched diets from fish to anurans at specific SVL sizes while *N. rhombifera* and *N. cyclopion* were mostly piscivorous but gradually altered the taxonomic composition of fish ingested with increasing size. Additionally, Miller and Mushinsky (1990) described *N. fasciata compressicauda* to be completely piscivorous with adult snakes selecting a different array of prey species than juvenile conspecifics. We observed *N. harteri* to display a similar pattern in which subadults primarily ingested minnows while adults utilized a greater variety of sizes and taxa of fishes.

Previous research has suggested that snake prey preferences vary geographically in response to regional differences in availability of prey types (Arnold, 1977, 1981). Mushinsky et al. (1982) further suggested that the ontogenetic dietary shift from fish to anurans observed in *Nerodia erythrogaster* and *N. fasciata* in Louisiana evolved due to the dependability of anurans as a food source. Although anurans (*Acris crepitans*, *Rana berlandieri*) were observed relatively frequently at our study sites they were infrequently ingested by Concho water snakes. We did

not monitor anuran populations at our study sites. However, our study areas are contained within a fairly drought prone, semi-arid region which could produce considerable annual variation in anuran densities. Fluctuation in the availability of anuran prey could promote selection for a piscivorous diet.

Although no abrupt ontogenetic diet shift was observed, there was a gradual change in the fish species utilized. This change was related to the absolute size of available prey species in relation to snake body size. Juvenile snake diets are often limited to a fraction of the prey available to adult conspecifics due to morphological constraints on ingestive capacity (Mushinsky, 1987). The restricted number of suitably sized prey types available to neonate and juvenile snakes probably accounts for the relatively low dietary diversity within these size classes. However, the number of ingestible prey types increases with snake body size allowing larger snakes to utilize a greater range of prey sizes and taxa. This resulted in the largest snakes, adult females, preferring the largest of the available prey species while also exhibiting the greatest dietary diversity.

The tendency of larger snakes to ingest larger prey indicates prey size discrimination. Foraging theory predicts that predators with access to a variety of prey sizes should select larger prey when they are sufficiently dense, thereby maximizing foraging efficiency (Schoener, 1971; Pyke et al., 1977). However, some empirical studies of snake diets have suggested that prey density and availability may also influence prey size selection (Voris and Moffett, 1981; Plummer and Goy, 1984; Shine, 1987). We propose that the numerical dominance of minnows relative to other prey types in this study probably explains the ingestion of numerous small prey. Additionally, the use of a stationary foraging technique may facilitate utilization of small, densely aggregated prey which may be efficiently harvested in this manner (Rose, 1989; pers. obs.).

Ontogenetic dietary shifts may result in associated changes in foraging techniques or foraging sites. Mushinsky et al. (1982) suggested that the foraging techniques of *Nerodia* in southern Louisiana should change ontogenetically to accommodate habitat preferences of different prey. Our observations of *N. h. paucimaculata* suggest that individuals of all sizes forage in riffles but utilize different techniques or foraging sites. These differences could be related to prey size selection since the larger prey species are associated with deeper water. However, minnows occur throughout riffles (pers. obs.) including deeper areas where small snakes do not forage. This may reflect an inability of juveniles to forage in deeper and swifter water

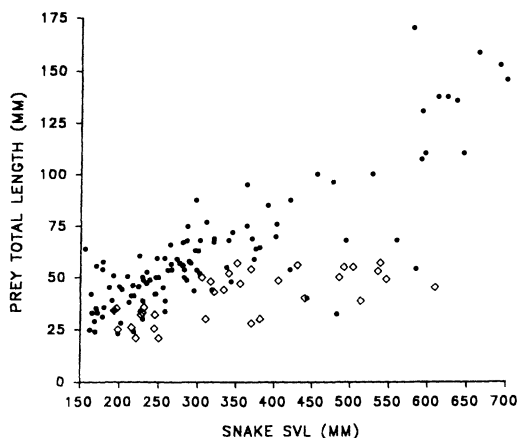


FIG. 1. Prey total length relative to snake SVL for individual *N. h. paucimaculata*. Solid dots represent single prey items from individual stomachs. Open squares represent the largest prey item from stomachs containing multiple prey (individual prey: Kendall's Tau = 0.59, $P < 0.001$, $N = 104$; largest item in multiple prey sample: Kendall's Tau = 0.43, $N = 33$; all items: Kendall's Tau = 0.46, $P < 0.001$, $N = 137$).

due to reduced physiological endurance compared with adult conspecifics (Pough, 1978).

Dietary differences between riverine and lacustrine snakes were influenced by prey abundance and habitat preferences of prey taxa in each system. Previous studies have implicated site-specific prey composition as a causal factor of diet variation among local populations (Gregory, 1978; Kephart, 1982). In this study many of the same prey taxa were present in both systems but were consumed in different proportions relative to their abundance. Neonate and juvenile snakes from riverine sites generally consumed the most abundant prey in proportion to abundance. However, lacustrine snakes largely ignored the most abundant potential prey, centrarchids and atherinids, which comprised roughly 65% of the potential prey sampled (Table 3). These taxa predominantly inhabit open water situations while the only prey ingested more frequently than expected (Percidae) were benthic (Pflieger, 1975; Robison and Buchanan, 1988). This pattern is not a consequence of prey size selection because many of the centrarchids and atherinids collected in prey samples were comparable in size to more frequently ingested prey taxa. Apparently, the catchability of individual prey species is influenced by their habitat preferences and (or) the foraging behavior of *N. h. paucimaculata* in lacustrine systems.

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LITERATURE CITED

- ANDREWS, R. M. 1982. Patterns of growth in reptiles. In C. Gans and F. H. Pough (eds.), *Biology of the Reptilia*, pp. 273-312. Academic Press, London.
- ARNOLD, S. J. 1977. Polymorphism and geographic variation in the feeding behavior of the garter snake *Thamnophis elegans*. *Science* 197:676-678.
- . 1981. The microevolution of feeding behavior. In A. Kamil and T. Sargent (eds.), *Foraging Behavior: Ecological, Ethological, and Psychological Approaches*, pp. 409-453. Garland Press, New York.
- BROWN, W. S., AND W. S. PARKER. 1982. Niche dimensions and resource partitioning in a Great Basin desert snake community. In N. J. Scott, Jr. (ed.), *Herpetological Communities*. U.S. Fish Wildl. Serv. Res. Rep. 13:59-81.
- BYERS, C. R., AND R. K. STEINHORST. 1984. Classification of a technique for analysis of utilization-availability data. *J. Wildl. Manage.* 48:1050-1053.
- DRUMMOND, H. M. 1979. Stimulus control of amphibious predation in the northern water snake (*Nerodia s. sipedon*). *Z. Tierpsychol.* 50:18-44.
- FITCH, H. S. 1987. Collecting and life-history techniques. In R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 143-164. Macmillan, New York.
- GILLINGHAM, J. D., AND T. RUSH. 1974. Notes on the fishing behavior of water snakes. *J. Herpetol.* 8:384-385.
- GREENE, H. W. 1983. Dietary correlates of the origin and radiation of snakes. *Amer. Zool.* 23:431-441.
- GREGORY, P. T. 1978. Feeding habits and diet overlap of three species of garter snakes (*Thamnophis*) on Vancouver Island. *Can. J. Zool.* 56:1967-1974.
- . 1984. Habitat, diet, and composition of assemblages of garter snakes (*Thamnophis*) at eight sites on Vancouver Island. *Can. J. Zool.* 62:2013-2022.
- GRIFFITHS, J., AND J. BRYAN. 1987. The Climates of Texas Counties. Dept. of Meteorology, College of Geosciences, Texas A&M Univ., Monograph Series No. 2. 569 pp.
- HENDERSON, R. W. 1982. Trophic relationships and foraging strategies of some new world tree snakes (*Leptophis*, *Oxybelis*, *Uromacer*). *Amphibia-Reptilia* 3:71-80.
- HUTCHESON, K. 1970. A test for comparing diversities based on the Shannon formula. *J. Theor. Biol.* 29:151-154.
- KEPHART, D. G. 1982. Microgeographic variation in the diets of garter snakes. *Oecologia* (Berlin) 52: 287-291.
- MILLER, D. E., AND H. R. MUSHINSKY. 1990. Foraging ecology and prey size in the mangrove water snake *Nerodia fasciata compressicauda*. *Copeia* 1990:1099-1106.
- MUSHINSKY, H. R. 1987. Foraging ecology. In R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 302-334. Macmillan, New York.
- , AND J. J. HEBBARD. 1977. Food partitioning by five species of water snakes in Louisiana. *Herpetologica* 33:162-166.
- , AND D. S. VODOPICH. 1982. Ontogeny of water snake foraging ecology. *Ecology* 63:1624-1629.
- NEU, C. W., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38:541-545.
- PFLIEGER, W. L. 1975. The Fishes of Missouri. Missouri Dept. of Conservation, Jefferson City. 343 pp.
- PIANKA, E. R. 1986. *Ecology and Natural History of Desert Lizards*. Princeton Univ. Press, Princeton, New Jersey. 208 pp.
- PLUMMER, M. V., AND J. M. GOY. 1984. Ontogenetic dietary shift of water snakes (*Nerodia rhombifera*) in a fish hatchery. *Copeia* 1984:550-552.
- POUGH, F. H. 1978. Ontogenetic changes in endurance in water snakes (*Natrix sipedon*): physiological correlates and ecological consequences. *Copeia* 1978:69-75.
- , AND J. D. GROVES. 1983. Specializations in the body form and food habits of snakes. *Amer. Zool.* 23:443-454.
- PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* 52:137-154.
- ROBISON, H. W., AND T. M. BUCHANAN. 1988. *Fishes of Arkansas*. Univ. of Arkansas Press, Fayetteville. 608 pp.
- ROSE, F. 1989. Aspects of the biology of the Concho water snake. *Texas J. Sci.* 41:115-130.
- SCHOENER, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704-726.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2:369-404.
- SCOTT, N. J., JR., T. C. MAXWELL, O. W. THORNTON, JR., L. A. FITZGERALD, AND J. W. FLURY. 1989. Distribution, habitat, and future of Harter's water snake, *Nerodia harteri*, in Texas. *J. Herpetol.* 23:373-389.
- SEIGEL, R. A., AND N. B. FORD. 1987. Reproductive ecology. In R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 210-252. Macmillan, New York.
- SHINE, R. 1987. Ecological ramifications of prey size: food habits and reproductive biology of Australian copperhead snakes. *J. Herpetol.* 27:21-28.
- VORIS, H. K., AND M. W. MOFFETT. 1981. Size and proportion relationship between the beaked sea snake and its prey. *Biotropica* 13:15-19.
- WALLACE, R. L., AND L. V. DILLER. 1990. Feeding ecology of the rattlesnake, *Crotalus viridis oreganus*, in northern Idaho. *J. Herpetol.* 24:246-253.
- WILLIAMS, N. R. 1969. Population ecology of *Natrix harteri*. Unpubl. M.S. Thesis, Texas Tech Univ., Lubbock. 51 pp.
- ZAR, J. H. 1984. *Biostatistical Analysis*, 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey.