

JOURNAL OF HERPETOLOGY

Foraging Time Investment in an Urban Population of Watersnakes (*Nerodia sipedon*)

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ABSTRACT.—In applying foraging theory to cryptic predators like many snakes, one of the most difficult variables to measure is effort spent in foraging. We estimated foraging effort from time invested in foraging using records for habitat use accumulated over a period of three years for 50 radio-tracked adult watersnakes (*Nerodia sipedon*). Because watersnakes eat predominantly aquatic prey, and limited prey records for the population studied were all fish, time spent foraging was estimated from the number of records in which snakes were found in water compared to the total number of records. Based on the data collected, this population of watersnakes devoted 1.43–2.38% of its time to foraging. Although the data do not permit allocation of foraging effort for most snakes to specific times, combining all relocation data suggests that adult watersnakes in this population forage infrequently. Opportunistic records of stomach contents regurgitated by captured snakes of all sizes suggest that these watersnakes find fish prey by active foraging and that the adult population benefits from periodic exploitation of dead or dying large fish (trout) following stocking.

Foraging theory assumes that animals attempt to maximize caloric and critical resource intake while minimizing the energy expended to acquire these resources. The net result of this strategy should be to provide more energy for reproduction, hence maximizing fitness (e.g., Stephens and Krebs, 1986; Perry and Pianka, 1997). Applying the theory to any particular species requires, among other things, direct or indirect measures of foraging effort. For cryptic predators, even simple measures, such as time spent foraging, can be extraordinarily difficult to measure in the field, although a common perception is that “most wild animals must spend a large fraction of their waking hours locating food and extracting it from their environments” (Griffin, 1992). Here we provide one indirect measure of foraging effort for one population of snakes that suggests this perception may apply less widely than thought.

For most snake species, foraging time or effort is difficult to measure because the snake spends most of its time in the same habitat as the prey. Most snake species are terrestrial, and their distribution in the environment overlaps that of their prey in complex ways. Movements of some species are infrequent (e.g., Greene, 1992; Greene and Santana, 1983) and assumed to involve finding patches where high density of preferred prey increases the probability that one prey individual will move close enough to be captured (Mushinsky, 1987; Beaupre and Montgomery, 2007). Foraging effort, in this case, would involve the cost of finding an appropriate patch and the cost of maintaining awareness and an ambush posture. Among the few measures of the times spent moving and ambushing are those of Clark (2006) using continuous video recordings of rattlesnakes. Other species of snakes move frequently and are assumed to be active foragers. However, they are difficult to track (e.g., Parker and Brown, 1980) and, for logistical reasons, most recent studies on their foraging ecology continue to deal only with snake and prey relationships. Relative predator and prey sizes, types, and spatial distribution have been measured (e.g., King et al., 2006; Halstead et al., 2008); and some field studies also have explored predatory behavior, including the sensory basis of prey capture (Hayes and Duvall, 1991; Shine et al., 2004a) but not time devoted to foraging.

Foraging behavior is linked to prey selection. Although snakes are constrained to swallowing prey whole (Gans, 1961; Cundall and Greene, 2000), *Nerodia*, like many macrostomatian snake species, can potentially satisfy its annual energetic demands by consuming a few relatively large prey (e.g., Carpenter, 1952; Reinert et al., 1984; Shine et al., 2004a,b). However, snake species capable of feeding on relatively large prey may opportunistically take prey of many sizes (e.g., Miller and Mushinsky, 1990; Arnold, 1993; Vincent et al., 2005). Gaining a measure of foraging effort can provide clues to the behavioral strategies used by populations to exploit available food resources.

In terrestrial environments, snakes are exposed to wide variety of potential prey that may be captured opportunistically at any time. Thus, simply knowing the location of a terrestrial snake tells little about its feeding behavior unless it feeds only on a limited variety of prey whose approximate distribution or density in the environment is also known. Opportunistic observations of field encounters between snakes and their prey occur infrequently but have provided most of the

detailed field data on foraging (e.g., Secor, 1995; Beaupre and Montgomery, 2007; Halstead et al., 2008). Much of what we know about foraging of terrestrial snake species comes from stomach contents of captured or dead snakes (e.g., Greene, 1997; Rodríguez-Robles, 2002).

Unlike snakes in terrestrial environments, many semiaquatic or arboreal snakes feed on prey that occur in only part of the space they occupy. Prolonged, quantitative observations of foraging have been made on ambush predation by some *Epicrates* on bats (Puente-Rolon and Bird-Pico, 2004) and in *Morelia viridis* ambushing rodents, birds, lizards, and insects (Wilson, 2007). Although some marine (Ineich and Laboute, 2002; Shine et al., 2004b) and freshwater snake species (Greene et al., 1994; Shine et al., 2004a) also have been studied, estimates of their foraging efforts have not yet emerged.

Adult Northern Watersnakes (*Nerodia sipedon*) feed predominantly on fish and amphibians, in some localities predominantly on amphibians (Palmer and Braswell, 1995), in others almost exclusively on fish (Gibbons and Dorcas, 2004; King et al., 2006, 2008). To catch fish and many of the amphibian species commonly taken, watersnakes usually must be in or near water (Brown and Weatherhead, 2000). As for most predators, their population densities reflect available prey densities (King et al., 2008). *Nerodia sipedon* grows large enough to take injured or diseased game fish, and it will also eat carrion, including parts of fish carcasses discarded by fishers.

We radio-tracked watersnakes for three activity seasons along a stocked trout stream in eastern Pennsylvania. We recorded their locations, selected habitat features, and general behavior. This analysis derives from our observations of habitat features at their locations.

MATERIALS AND METHODS

We radio-tracked 50 *N. sipedon* between 23 May 2004 and the end of October 2006, along Monocacy Creek, a fourth-order stream flowing through the eastern Pennsylvania city of Bethlehem. The stream bank and adjacent land were considered natural (second growth forest on vegetated floodplain) for the approximate middle half of the study site and urbanized at the northern (mowed lawn, municipal park) and southern (industrial buildings and warehouses, paved lots) ends (Pattishall and Cundall, 2008, 2009). Snakes were rarely found more than 20 m away from the stream (12% of relocations), and only 3% of snake-selected sites were more than 50 m from the stream. Following a major flood event in 2004, one snake was found 100 m from the normal stream course, the greatest distance measured. The stream itself is spring-fed and has a temperature range of 10–19°C when the snakes are active, about 7–18°C below the preferred body temperatures of *N. sipedon* in southern Ontario (Robertson and Weatherhead, 1992). Based on electro-fishing surveys by the Pennsylvania Fish and Boat Commission, other reaches of the stream support a variety of fish species (e.g., *Cottus cognatus*, *Etheostoma olmstedi*, *Fundulus diaphanus*, *Pimephales notatus*, *Rhinichthys atratulus*, *Semotilus atromaculatus*, *Catostomus commersoni*), including native (Brook Trout, *Salvelinus fontinalis*) and introduced (Brown Trout, *Salmo trutta*) trout. A small permanent pond located at the western edge of the study site contains carp, sunfish (*Lepomis*, mostly *macrochirus*) species, and tadpoles (*Lithobates catesbeianus*).

During the three-year study, we recorded substrate characteristics of every location where radio-tagged snakes were found and the behavior

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TABLE 1. Relocations of snakes in, above, or near water, moving or not, by sex and reproductive condition.

	Total relocations	In water		<1 m from water or above water		<1 m from water and moving		Moving anywhere	
		#	%	#	%	#	%	#	%
Male	391	8	2.03	189	48.34	6	1.53	16	4.09
Gravid female	984	12	1.22	188	19.11	3	0.30	24	2.43
Nongravid female	1,145	16	1.48	446	38.95	2	0.17	20	1.75
Totals	2,520	36	1.43	823	32.66	11	0.44	60	2.38

of the snake when first found. Additionally, we recorded a variety of behavioral and habitat features (Pattishall and Cundall, 2009). The most important of these for foraging measures are time of day, day of year, distance from water, substrate type, water temperature, and behavior when seen. Also, we recorded all prey regurgitated by snakes upon capture for transmitter implantation or replacement, all prey observed being eaten in the field, and all watersnakes with observable enlargements of their stomachs, indicative of recent feeding on large prey.

The effects of reproductive state and sex on foraging behavior were examined by comparing substrate records for males, and nongravid and gravid females. To test the potential relationship between sex or reproductive condition and the timing of foraging, we tested effects of time of day and calendar day with Kruskal-Wallis ANOVA. Feeding is thought to occur infrequently if at all during the mating season, which usually ends at the beginning of June, but all watersnakes, including gravid females, may feed during the remainder of the active season (Aldridge and Bufalino, 2003). To determine relative condition, all watersnakes were measured and weighed when captured for transmitter implantation or replacement.

To test whether watersnakes moved or foraged outside normal daylight hours when most tracking and relocations were made, we periodically relocated snakes throughout the 24-h period during the warmer part of the active season (early May to early October). Then we compared the data collected in the 10-h "dark" period between 2000 and 0600 h with an equivalent number of randomly selected relocations taken in the 14-h "daylight" period between 0600 and 2000 h.

Although watersnakes are known to take a wide variety of prey, in some populations studied carefully (King et al., 2006, 2008; Jones et al., 2009) the majority of prey are fish. Snakes in our population were known to take dead or dying fish, some of which occurred at the edge of the stream. Therefore, we examined all records for snakes found within 1 m of water and used activity records to estimate foraging possibility. Also, we recorded the presence of potential prey and predator species at the study site and searched for neonate watersnakes from August until the snakes disappeared into hibernacula.

RESULTS

We located radio-tagged snakes 2,520 times over the three years. The earliest recorded snake location was 11 March 2006, the latest 25 October 2005 (Pattishall and Cundall, 2008). As noted previously (Pattishall and Cundall, 2009), snakes were found repeatedly at a limited number (113) of sites. Only 36 of the 2,520 relocations were in

water (Table 1). Of 823 relocations within 1 m of water, only 11 of the behavioral records listed the snake as moving or foraging. Taking all the data for all sites, 60 were recorded as moving or foraging. Because the only prey recovered from snakes in this population were fish, we assume that in-water sites represent the most likely foraging sites. Hence, a possible time spent foraging was 36/2,520 or 1.43% of the total time available to the snakes (2.40 h/week). Of the 11 relocations of moving snakes within 1 m of water, one overlaps the in-water records. Hence, adding 10 relocations to the 36 would give a foraging effort of 46/2,520 or 1.83% (3.07 h/week). Assuming that all moving snakes were actually foraging, the maximum foraging effort amounted to 2.38% of available time or 4.00 h/week. However, the watersnakes in our population used the stream environment during courtship, mating, making long-distance moves, as well as foraging. Thus, like the situation quantified by Clark (2006) in which timber rattlesnakes in "foraging" posture actually struck at only 25% of the prey passing in their vicinity, our time estimates, including those for the in-water sites, likely represent the maximum times the snakes could have been foraging.

Males contributed disproportionately to the in-water records (Table 1), but examining the dates and field notes associated with these records suggests that two of these were for males swimming during the mating season and seemingly searching for females not food. There were no significant differences between sexes or reproductive conditions for time of day or day of year when foraging occurred.

As expected from the small number of in-water relocations, eight of 14 males and 26 of 36 females were never relocated in water. The only evidence that these snakes ate is that their condition did not change detectably. Three of the four females that carried functioning transmitters for three years were gravid every year. Weights of individual snakes varied considerably depending on when they were weighed relative to reproductive condition and, presumably, feeding (Table 2). Females may lose a third or more of their gravid weight at parturition (snakes 9 and 36), and generally those caught in the spring for transmitter replacement weighed less than they did during the activity season of the previous year (snakes 11, 15, 19). Of nine snakes that regurgitated prey, all were females, four caught in April or May, three in the first 10 days of June, one in late June, and one in mid-September. All but two contained only trout or trout parts. One from late April regurgitated five sculpins (*Cottus cognatus*) and the one in mid-September (2005) a large (220 g) sucker (*Catostomus commersoni*). The condition of all but a few snakes that died during the study (snakes

TABLE 2. Snake mass, reproductive condition (RC, gravid [G] or nongravid [NG]), and length (cm) over time for snakes relocated for two or three years. t = transmitter ceased functioning shortly after implantation in 2004—antenna detached. * = snake died before end of study.

Snake #	Sex	2004				2005				2006			
		RC	Mass	Date	SVL	RC	Mass	Date	SVL	RC	Mass	Date	SVL
9	F	G	401	7/14	75	NG	310	6/24	76				
10	F*	G	224	6/11	66		260	6/2	72				
11	F	t	229	6/17	63	G	211	5/16	65	G	267	4/27	69
12	F	G	340	6/16	71	G	381	9/19	76	G	315	5/17	77
15	F	G	458	7/19	76	G	390	5/12	79				
16	F	G	351	7/22	74	G	299	6/28	75	G	438	5/5	77
17	M		200	10/5	60		171		60				
19	F	NG	320	10/6	72	NG	279	6/2	71	NG	177	3/30	71
21	F					G	208	4/26	60	G	252	6/19	64
24	F					G	421	5/4	77		353	5/18	77
31	F					NG	115	5/27	54	G	136	5/9	57
36	F*					G	311	7/14	65	NG	177	3/11	63
37	M*						145	9/19	61		141	3/11	62

10, 36, 37) was good, and for most of the snakes, their weight and appearance did not change noticeably (Table 2), suggesting that they were eating.

Observations made at night suggest that snakes spent no more time foraging than during the day. Of 140 night-time (2000–0600 h) relocations, only two were for snakes in water (1.43%), identical to the proportion arrived at for the entire data set, and neither was recorded as foraging. Interestingly, if the night-time samples are compared to a random sample of 140 daytime (0600–2000 h) relocations, the substrate was water for only two of these as well.

DISCUSSION

For opportunistic predators, foraging effort must relate to the distribution and nature of their prey and their intrinsic abilities to detect and catch acceptable prey. In those unusual circumstances in which the prey do not occupy the same medium normally occupied by the predator, as is the case for some fish-eating “specialists” among advanced snakes, one can assume that all of the time spent outside the prey’s medium is not spent foraging and that some of the time these predators spend in the medium of their prey—in this case, water—is devoted to finding prey (Brown and Weatherhead, 2000; Nelson and Gregory, 2000; King et al., 2006). Watersnakes in our study regurgitated only fish. At our study site, we have also assumed that watersnakes make longer distance movements within their activity range using the stream course (Pattishall and Cundall, 2008). For watersnakes, the major other reasons for being in water may be thermoregulation (Brown and Weatherhead, 2000) or avoidance or escape from their own predators, particularly human and some avian predators. Given the nature of our study, the small number of relocations of snakes actually in water invites several possible interpretations.

First, it is unlikely that all in-water relocations were associated with foraging. For example, two in-water relocations for males made during the mating season (late April through May) could have represented searching for females rather than food. Similarly, the probability that snakes at locations within 1 m of the stream were foraging is small. First, the potential prey in this location would be fish or fish parts discarded by fishers, dead fish, and amphibians. Frog populations along Monocacy Creek are limited primarily to *Lithobates catesbeianus*, *Lithobates palustris*, *Lithobates pipiens*, and *Anaxyrus americanus*. Frogs were seen regularly at only a few sites along the stream, possibly because there are few ponds in the vicinity. The large pond at the southwestern edge of the natural area contains *L. catesbeianus* tadpoles, but daily walking of the pond and stream banks revealed few adult frogs. No snakes regurgitated frogs or frog parts. One implanted watersnake was seen in the water in this pond and a number of implanted watersnakes basked in the bushes along its eastern bank closest to the stream. Other amphibian species are present, but the larger aquatic salamander species that overlap the range of *N. sipedon* (*Ambystoma*, *Necturus*) do not occur at our site. The smaller salamander species recorded as prey of *N. sipedon* (*Plethodon cinereus*, *Eurycea bislineata*, *Desmognathus fuscus*) occur at our site, but we have no evidence that adult watersnakes in our population ate them or devoted any time to searching for them.

Watersnakes can and will catch prey in terrestrial settings in captivity (Cundall, 1983; Cundall and Gans, 1979; video and cine records of *Nerodia* catching live fish from the floor of a cage) but they apparently do so infrequently in the field (Gibbons and Dorcas, 2004). Extensive literature records for feeding in this species suggest it is an aquatic fish and amphibian generalist that might eat most of the fish and amphibian species common in and around Monocacy Creek (Gibbons and Dorcas, 2004). However, the majority of sites occupied by adult watersnakes relocated in this study are terrestrial or arboreal in areas in which no fish and few amphibian species occur. Our argument is based on the absence of evidence of watersnakes foraging on species other than fish and the small number of records of snakes recorded as moving or foraging when seen compared to the total number of relocations.

One factor that might limit the amount of time spent in water other than that allocated to foraging in this species is the low temperature of the water in Monocacy Creek. Although we observed some snakes foraging under water for periods of more than 15 min, the small number of in-water observations suggests that, as for *Thamnophis sirtalis* at a fish hatchery (Nelson and Gregory, 2000), the snakes are minimizing the amount of time spent in water.

In summary, our data suggest that watersnakes in this urban stream can find prey sufficient to support continued reproduction by active foraging for a remarkably small percentage of their time. Also, our data

suggest that food is not limiting for this population and that the snakes either find small prey very quickly or find large prey often enough to allow infrequent movements. Regurgitated prey show that both strategies are used. As previously suggested (Pattishall and Cundall, 2008, 2009), the snakes in this population move infrequently and repeatedly use relatively few sites. How this population differs from other populations of *N. sipedon* in its foraging behavior remains unclear. There are no comparable comparative data. However, our field experiences at other sites and the collective literature suggest to us that this population’s foraging effort may lie near the extreme lower end of a range.

Acknowledgments.—We thank H. Reinert for his advice on transmitter implantations and H. Greene, T. Mendelson, B. Hargreaves, and J. Schneider for their critical evaluations of this project. This paper grew out of data collected by AP for her doctoral dissertation submitted to the Department of Biological Sciences, Lehigh University. J. Sharkan and D. Vash of Pennsylvania Perlite Corp. and G. Beitelman of Quiet Core, Inc. provided access to their properties and information on the use of their properties by watersnakes. K. Keating and C. Zambrano provided essential field support to AP during night-time tracking while they were undergraduates at Lehigh University. Animals were collected under Pennsylvania Fish and Boat Commission Permit 070 issued to DC and radio transmitters were implanted under Lehigh University IACUC protocol A3877-01.

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Accepted: 17 August 2010.