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; Beaurpe 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 macrostomatan 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 (Gans, 1961; Mushinsky, 1987; 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 a 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; Beaurpe 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; Rodriguez-Robles, 2002).

Unlike snakes in terrestrial environments, many semiaquatic or arboreal snake species 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 Epecrates on bats (Puente-Rolon and Bird-Pico, 2004) and in Morelia viridis ambush 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, 2008). 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 fishermen.

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 (Roberson 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, Pimelophus notatus, Rhamichthys atratulus, Semotilus atromaculatus, Catas- tamus comersoni), 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 microchirus) 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

2 Corresponding Author.
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; Vonesh 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 overlapped 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 foraging5 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 1). 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 commersonii).

The condition of all but a few snakes that died during the study (snakes

<table>
<thead>
<tr>
<th>Snake #</th>
<th>Sex</th>
<th>RC</th>
<th>Mass</th>
<th>Date</th>
<th>SVL</th>
<th>RC</th>
<th>Mass</th>
<th>Date</th>
<th>SVL</th>
<th>RC</th>
<th>Mass</th>
<th>Date</th>
<th>SVL</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>F</td>
<td>G</td>
<td>401</td>
<td>7/14</td>
<td>75</td>
<td>NG</td>
<td>310</td>
<td>6/24</td>
<td>76</td>
<td>10</td>
<td>F</td>
<td>G</td>
<td>224</td>
</tr>
<tr>
<td>10</td>
<td>F*</td>
<td>G</td>
<td>224</td>
<td>6/11</td>
<td>66</td>
<td>260</td>
<td>6/2</td>
<td>72</td>
<td></td>
<td>11</td>
<td>F</td>
<td>G</td>
<td>229</td>
</tr>
<tr>
<td>12</td>
<td>F</td>
<td>G</td>
<td>340</td>
<td>6/16</td>
<td>71</td>
<td>G</td>
<td>211</td>
<td>5/16</td>
<td>65</td>
<td>15</td>
<td>F</td>
<td>G</td>
<td>458</td>
</tr>
<tr>
<td>15</td>
<td>F</td>
<td>G</td>
<td>458</td>
<td>7/19</td>
<td>76</td>
<td>G</td>
<td>381</td>
<td>9/19</td>
<td>76</td>
<td>16</td>
<td>F</td>
<td>G</td>
<td>351</td>
</tr>
<tr>
<td>17</td>
<td>M</td>
<td>G</td>
<td>200</td>
<td>10/5</td>
<td>60</td>
<td>G</td>
<td>299</td>
<td>6/25</td>
<td>75</td>
<td>19</td>
<td>F</td>
<td>NG</td>
<td>320</td>
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<td>21</td>
<td>F</td>
<td>G</td>
<td>208</td>
<td>4/26</td>
<td>60</td>
<td>G</td>
<td>252</td>
<td>6/19</td>
<td>64</td>
<td>24</td>
<td>F</td>
<td>G</td>
<td>421</td>
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<tr>
<td>31</td>
<td>F</td>
<td>NG</td>
<td>115</td>
<td>5/27</td>
<td>54</td>
<td>G</td>
<td>136</td>
<td>5/9</td>
<td>57</td>
<td>36</td>
<td>F</td>
<td>G</td>
<td>311</td>
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<td>G</td>
<td>177</td>
<td>3/11</td>
<td>63</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Total relocations</th>
<th>In water</th>
<th>&lt;1 m from water or above water</th>
<th>&lt;1 m from water and moving</th>
<th>Moving anywhere</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>391</td>
<td>8</td>
<td>2.03</td>
<td>189</td>
</tr>
<tr>
<td>Gravid female</td>
<td>984</td>
<td>12</td>
<td>1.22</td>
<td>188</td>
</tr>
<tr>
<td>Nongravid female</td>
<td>1,145</td>
<td>16</td>
<td>1.48</td>
<td>446</td>
</tr>
<tr>
<td>Totals</td>
<td>2,520</td>
<td>36</td>
<td>1.43</td>
<td>823</td>
</tr>
</tbody>
</table>


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