

Fixed Videography to Study Predation Behavior of an Ambush Foraging Snake, *Crotalus horridus*

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Our ability to understand predator-prey systems is often limited by a lack of detailed information on fundamental aspects of organismal natural history. It is particularly difficult to gather quantitative data on the behavior of sit-and-wait predators, which are generally secretive and feed infrequently. In this study I use video surveillance equipment to record natural interactions between a predator, *Crotalus horridus*, and its prey. From observations of 17 individuals over two years, a total of 87 encounters with prey were recorded, with snakes successfully attacking 13% of prey items that came within striking distance. Snakes stayed at ambush sites for a mean of 17 hours and were estimated to feed between 12 and 15 times over the course of a season, consuming between 1250 and 1550 g of prey per snake, mostly woodland rodents (*Peromyscus*, *Microtus*, *Clethrionomys*, *Tamias*, and *Sciurus*). These data represent some of the most detailed quantitative measures on snake foraging behavior and predator-prey interactions available and can be used to inform general ecological and behavioral models in similar systems.

ECOLOGICAL and behavioral research is often limited by our knowledge of an organism's natural history. For example, population viability analyses rely on knowledge of reproductive behaviors and social systems (Beissinger and McCullough, 2002), measures of habitat suitability need to evaluate microhabitat usage and animal movement patterns (Gurnell et al., 2002), and ecological and physiological models of predatory behavior are most effective when actual measures of an organism's feeding rate are known (Beaupre, 2002).

Predation plays a central role in ecological and evolutionary research in areas as diverse as ecological physiology (Beaupre and Duvall, 1998), coevolutionary arms races (Brodie and Brodie, 1999), and ecosystem dynamics (Duffy, 2003). However, in many systems predation is difficult to observe under natural conditions. Consequently, our understanding of predation-based phenomena is often limited to laboratory studies and anecdotes. Shine et al. (2004) recently argued that snakes are representative of a group in which field studies on predation are extremely rare, even though adaptations related to predation have played a central role in the evolutionary diversification of snakes. Instead, our knowledge of their foraging behavior stems from laboratory studies, anecdotal observations, morphological analyses, and dietary analysis.

Many snakes are sit-and-wait foragers, a tactic often employed by sedentary, cryptic predators that rely on ambush to capture their prey (Schoener, 1971; Huey and Pianka, 1981). Because ambush predators feed infrequently, it is usually not feasible for researchers to collect

information on their natural prey encounters directly. However, it is possible to take advantage of their sedentary feeding behavior and use fixed videography to record predation behavior indirectly, similar to the way in which researchers have recently begun monitoring nest predation in birds (McQuillen and Brewer, 2000; Stake and Cimprich, 2003). I apply this technique to study the foraging behavior of Timber Rattlesnakes (*Crotalus horridus*), a large viperid species widely distributed throughout the eastern United States. Throughout their range they feed almost exclusively on small mammals and birds (Clark, 2002). Like most viperids, they are ambush predators (Reinert et al., 1984), and natural prey encounters have been described only anecdotally. The fixed videography approach enables the collection of precise data on ambush foraging viperids, which may make them a model system for examining predator-prey interactions and foraging behavior. Resultant video recordings provide quantitative information on ambush site residence time, prey encounter rate, and predation success rate that would be extremely difficult to observe directly.

MATERIALS AND METHODS

Radio telemetry.—I tracked 17 adult individual Timber Rattlesnakes (11 females, 6 males) from May 2002 through October 2003 at a nature preserve in Chemung County, New York. Snakes were captured opportunistically throughout the study and ranged in size from 104–137 cm total length and 650–2100 g (mean TL = 121 ± 15 cm, mean wt = 1405 ± 640 g). Miniature

temperature-sensitive radio transmitters (Holohil Systems, models AI-2T and SI-2T) were surgically implanted in the peritoneal cavities of snakes under inhalation anesthesia (isoflourane), following the methods of Reinert and Cundall (1982). Transmitters weighed <5% of the snake's body mass. I returned snakes to their point of capture within 24 hours of surgery, and radio tracking began immediately. Individuals were located on a daily basis. Upon location, I recorded distance moved from last location, weather conditions, ambient temperature, and the snake's location, habitat use, body position, and body temperature. Distances less than 20 m were estimated manually to within two meters, while distances greater than 20 m were estimated to within five meters with the use of a handheld GPS unit.

Videography.—To collect data on foraging behavior, I trained video cameras on snakes that were in compact coils—a position in which they sit and wait for prey to come within striking distance. Three different video units were used concurrently in the field. Each unit consisted of a security camera coupled to a time-lapse videocassette recorder (Mobile 12 V Time Lapse Recorder Model NCL3300) powered by a 12-V sealed lead-acid battery. Cameras (High Resolution Color CCD IR, model BC 1035) recorded in color when ambient light was available and under low light conditions automatically switched to black and white recording with infrared LEDs. Time-lapse VCRs were set to record continuously at 6.67 recording frames per second, with the date and time to the nearest second displayed on the tape. I then reviewed tapes, and data were extracted on snake residence times and encounters with potential prey.

Specific methods for quantifying relevant variables were as follows: (1) Time. For each foraging site, I estimated the time at which the snake selected that site to the nearest hour. This time was not measured more precisely because the necessity of having to monitor several individuals concurrently meant that they could select a site while not being monitored. From the tapes, I noted the total number of daylight and nighttime hours spent at that site and the time at which the site was abandoned by the snake. (2) Prey identity. As *C. horridus* is known to feed on a wide variety of small birds and mammals (Clark, 2002), all small birds and mammals coming within 50 cm of a coiled snake were recorded as potential prey. I estimated the closest distance between the potential prey and the snake to the nearest ten centimeters. Prey items were identified to as fine a taxonomic level as

possible using video images, distribution data from Whitaker and Hamilton (1998), and a record of small rodents collected in live traps at the site (approximately 32 individuals from 20 trap nights). Approximate masses for these prey items were determined from the collection data of a random sample of ten adult individuals from New York deposited in the Cornell Vertebrate Collection. Prey items that were only identified as nocturnal rodents were assigned an approximate mass of 30 g, a rough mean for appropriate species from Whitaker and Hamilton (1998) that still allows for ecologically feasible calculations of prey mass consumption. (3) Snake behavior. The response of the snake was recorded as no strike, missed strike, or successful strike. Additionally, the subsequent response of snakes was noted as to whether or not they initiated strike-induced chemosensory searching (SICS) after successful strikes (Chiszar et al., 1977).

All values are given as mean \pm standard deviation. Data compared with parametric statistics were transformed for normality, where appropriate, using arcsin and square root transformations.

RESULTS

Snake foraging effort.—As is typical of *C. horridus* in the northeast (Brown, 1993), snakes were dispersed from their hibernacula for approximately 143 days, from the beginning of May until the last week of September. Snakes shed either once or twice a year, spending an average of 11 ± 4 days ($n = 17$) in basking habitat under pre-shed conditions, leaving an estimated 132 days of potential foraging.

Over the course of the study, I recorded snakes at putative ambush sites for a total of 1047 daytime hours and 793 nighttime hours. Snake residence times at a given ambush site ranged from 2 to 67 hours, with a mean of 17 ± 13.8 hours ($n = 88$, counting only those foraging bouts wherein the camera was set up within 1 hour of the snake finding an ambush site). Snakes typically changed ambush locations either shortly after dark (45% of site abandonments from 1900 to 2200) or during the middle of the day (27% of site abandonments from 1000 to 1400; Fig. 1). I made two estimates of time traveled between ambush sites. A minimum estimate of 1 ± 0.6 h ($n = 11$) was made from the mean time for all snake movements between sites that I observed directly. However, in the majority of cases, I was not able to monitor movements directly, and so a maximum estimate of 4 ± 2.9 h ($n = 88$) was made from the maximum amount of time lapsed between the

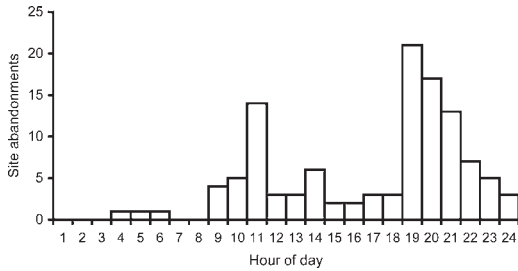


Fig. 1. Number of foraging site abandonments by time of day when *C. horridus* were observed to abandon foraging sites wherein no prey was encountered ($n = 114$).

snake abandoning its site (recorded from videotape) and the time of first observation at its new site.

The mean estimated distance between ambush sites was 47 ± 80.1 m, with a range of 1–900 m ($n = 88$). Movements between ambush sites were bimodal, with the majority of movement being under 20 m in length, but there were occasional long movements between successive sites (Fig. 2).

Prey encounters.—Encounters with prey took place mainly at morning and night (Fig. 3). A total of 87 encounters with potential prey were recorded, with 65 of them resulting in no strike on the part of the snake, 11 resulting in a missed strike, and 11 resulting in a successful strike. Thus, snakes successfully attacked a small proportion of potential prey that came within striking distance. In all cases, snakes that missed strikes remained at the ambush site, and snakes that succeeded in striking prey initiated SICS and trailed the prey in the direction in which it fled. In two cases, I was able to estimate the distance which envenomated prey traveled before stopping at 7 m and 0.75 m.

To examine the influence of ambient temperature on predation behavior, average daily temperature records were obtained from the weather station at the Elmira New York airport,

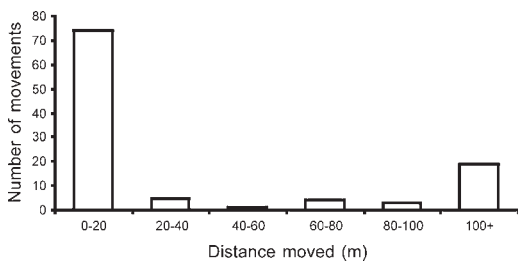


Fig. 2. Estimated distance moved by *C. horridus* between successive ambush sites ($n = 88$).

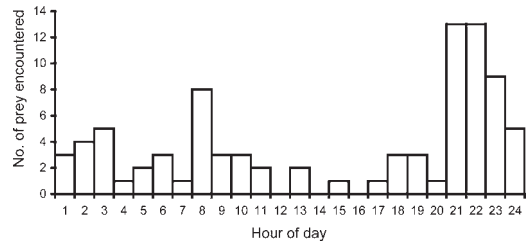


Fig. 3. Encounters of potential prey by time of day at which *C. horridus* were observed to encounter potential prey items ($n = 87$).

five miles away. Mean daily temperature was significantly higher on days where successful strikes occurred than on days wherein missed strikes or no strikes occurred (mean temperature on days with successful strikes was 20 ± 3.4 C ($n = 11$); mean temperature on days with missed or no strikes was 18 ± 4.1 C ($n = 76$; $T = 2.3$, $df = 15$, $P = 0.03$). This difference was not due to higher prey availability on warmer days, as there was no difference in temperature between days when no prey was encountered (18 ± 3.7 C, $n = 84$) versus days when prey was encountered (18 ± 4.3 C, $n = 87$, $T = 0.08$, $df = 120$, $P = 0.9$).

All potential prey were identified to species, with the exception of some small nocturnal rodents (Table 1). Nocturnal rodents present at the field site include white-footed mice (*Peromyscus leucopus*), deer mice (*P. maniculatus*), red-backed voles (*Clethrionomys gapperi*), and meadow voles (*Microtus pennsylvanicus*). These species, which are all similar in size, were identified under the category “nocturnal rodent” (Table 1). From these data, the average rate of successful nocturnal prey encounters was 0.1 prey items struck per night (nine successful encounters over approximately 80 observed nights foraging), and the average estimated size of

TABLE 1. IDENTITY OF ALL POTENTIAL PREY ITEMS ENCOUNTERED BY ACTIVELY FORAGING *C. horridus* AND OUTCOME OF PREDATORY ENCOUNTERS.

| Prey identity | Number encountered | Successful attacks | Approximate mass (g) |
|--|--------------------|--------------------|----------------------|
| Nocturnal rodent | 52 | 7 | 30 |
| Grey squirrel (<i>Sciurus carolinensis</i>) | 13 | 1 | 500 |
| Chipmunk (<i>Tamias striatus</i>) | 11 | 1 | 100 |
| Flying squirrel (<i>Glaucomys volans</i>) | 2 | 1 | 55 |
| Weasel (<i>Mustela frenata</i>) | 2 | 1 | 210 |
| Bird sp. | 5 | 0 | na |

TABLE 2. AVERAGE NUMBER OF PREY ITEMS CONSUMED BY *C. horridus* PER DAY AND PER NIGHT, AVERAGE ESTIMATED MASS OF THOSE PREY, AND ESTIMATED PREY MASS CONSUMED PER YEAR. See text for quantitative methods of estimation.

| | Number of prey consumed | Mean mass of prey (g) | Annual prey consumption (g) |
|---------------------------|----------------------------|--------------------------|--------------------------------|
| Daytime | 0.024 | 300 | 720–900 |
| Nighttime | 0.1 | 53 | 525–652 |
| Combined 24-hour total | 0.124 | 98 | 1245–1552 |

nocturnal prey items successfully attacked was 53 ± 59.5 g ($n = 7$). The average rate of successful diurnal prey encounters was 0.024 prey items struck per day (two successful encounters over approximately 75 observed days foraging), and the average estimated size of diurnal prey items successfully attacked was 300 ± 282.8 g ($n = 2$; Table 2). Snakes were actively foraging for approximately 132 total days at this site; from earlier estimates of time spent in moving between ambush position, snakes spent between 7% and 25% of active time not in ambush, leading to between 99 and 123 foraging days per year. With an average rate of 0.1 prey successfully attacked per night and 0.024 prey successfully attacked per day, snakes at this site were estimated to successfully attack between 12 and 15 prey items per year. Over one active season, between 2.4 and 3.0 diurnal prey were consumed, with an estimated average mass of 300 g, leading to an annual biomass consumption of between 720 and 900 g of diurnal prey. Similarly, between 9.9 and 12.3 nocturnal prey were consumed, with an average estimated mass of 53 g, leading to an annual biomass consumption of nocturnal prey between 525 and 652 g, and an estimate of total annual biomass consumption (diurnal and nocturnal prey) of between 1245–1552 g.

DISCUSSION

The results of this study provide a detailed analysis of the foraging behavior, prey encounter rate, and predatory success rate of free-ranging Timber Rattlesnakes. These results provide quantitative ecological information for a widely distributed top-level predator and show that fixed videography of ambush-foraging snakes can be used to obtain a relatively large sample of predation events. The number of events recorded here far exceeds what is available in the literature. Even within this short-term study, important patterns emerged that increase our

knowledge of viperid foraging strategies and predation rate.

My results indicate that Timber Rattlesnakes exhibit a two-stage prey finding strategy, similar to what was reported by Reinert et al. (1984). In the first stage, they move through the environment assessing potential ambush sites to find a site where they are likely to encounter appropriate prey relatively quickly. After selecting a site, they wait until either prey is encountered or until it is determined that further prey encounter is unlikely, at which point the site is abandoned. Other rattlesnake species have been reported to exhibit very similar strategies (Chiszar et al., 1990; Duvall et al., 1990; Roth et al., 1999).

Timber Rattlesnakes were found to exhibit a wide range of residence times at their ambush sites, from a few hours to several days, with a mean residence time of 17 h. Although Reinert et al. (1984) found a mean residence time of 7.3 h, their study focused only on eight observations of two individuals. This difference in residence time is within the range of variation reported in this study and probably does not reflect any intraspecific difference in foraging behavior. However, other viperid species, such as the Bushmaster (*Lachesis muta*) and the Chinese pit-viper (*Gloydius shedaoensis*), have been reported to wait at sites for much longer (Greene, 1986; Shine et al., 2002b); these differences may reflect interspecific variation in foraging strategies.

Timber Rattlesnakes appear to be choosing ambush sites where they may encounter multiple prey individuals, sometimes even different species. At approximately 7% of ambush sites, more than one species of prey was identified as they came within striking range. On three occasions, snakes returned to the same ambush location after striking prey, trailing it, and evidently consuming it; on six occasions, individuals of the same prey species were observed to come within striking range after a snake at that site had already struck at and missed a prey item, indicating that the prey animals were likely different individuals of the same species. Laboratory studies show that *C. horridus* is very sensitive to prey chemical cues (Clark, 2004a,b). Thus, they most likely use prey chemical trails to select those sites that are used by multiple individuals.

Timber Rattlesnakes struck at 25% of prey that came within their estimated strike radius. The tapes showed that a majority of potential prey items passed by too quickly for the snakes to respond. When snakes did strike, approximately 50% of those strikes missed the prey. This value is

consistent with observations by Shine et al. (2002b) indicating Chinese pit-vipers also exhibit a relatively high frequency of missed strikes. Even observations with captive mice conducted under laboratory conditions show that rattlesnakes frequently miss strikes (Chiszar et al., 1986; Kardong, 1986; Cundall and Beaupre, 2001). The strike is kinematically complex, requiring the coordination of several sensory modalities and movements (Kardong and Smith, 2002). The strike may be most effective under optimal conditions of ambush site selection, when snakes have the opportunity to detect approaching prey well before they come within striking range (Shine and Sun, 2002). In my study site, strike success may have been influenced by temperature, as indicated by the higher maximum temperature of days when successful strikes occurred. While other studies have also found that strike speed and success in viperid snakes is influenced by temperature (Shine et al., 2002a), a more detailed analysis on thermal correlates of predatory behavior could be conducted by combining the methods of this study with the implantation of miniature temperature loggers into the body cavities of free-ranging snakes (Angilletta and Krochmal, 2003).

The range of prey items encountered by these snakes is similar to their diet for this region (Reinert et al., 1984; Clark, 2002), with the exception of a long-tailed weasel (*Mustela frenata*), which is a previously unreported prey item. Laboratory studies indicate that *C. horridus* has an innate predisposition towards sympatric prey (Clark, 2004b), but also will respond to a wide variety of chemical cues from allopatric small mammals and will learn from experience to identify chemical cues associated with profitable feeding events (Clark, 2004a). Thus, dietary differences between sites will likely reflect variation in prey abundance.

Snakes at this site are estimated to have successfully attacked prey 12 to 15 times per year, consuming between 1245 and 1552 g of prey biomass (around 100% of body mass in annual prey consumption). Zaidan and Beaupre (2003) estimate that a 500-g *C. horridus* would require only approximately 280 grams of rodent per year to sustain itself. This discrepancy indicates that a large amount of excess energy is likely to be available for growth, fat storage, and reproduction. My estimate of annual prey consumption for *C. horridus* is consistent with estimates of between 91% and 98% of body mass in annual prey consumption for *C. atrox*, *C. tigris*, and *C. molossus*, which were based on energy budgets constructed by Beck (1995). They are also similar to estimates from the doubly labeled

water method for field metabolic rates of *C. lepidus* (between 113% and 193% of body mass in annual prey consumption; Beaupre, 1996), but somewhat lower than estimates for *C. cerastes* (220% of body mass in annual prey consumption; Secor and Nagy, 1994). Because the data in this study are based on a few individuals at this one site, they do not reflect the wide degree of temporal and geographic variability in prey availability that is likely to be present (e.g., Beaupre, 1996). Further studies will be required to characterize variation in foraging success between individuals, populations, and species.

The majority of feeding events in this study (81%) took place at night. This is likely because nocturnal small mammals in eastern deciduous forest occur at much higher densities than diurnal small mammals (Whitaker and Hamilton, 1998). However, the average per item mass of diurnal prey species was greater, leading to an approximately equal amount of estimated prey biomass consumed during both day and night. Therefore, both nocturnal and diurnal foraging is likely to be important to *C. horridus*.

The ambush-style predation strategy quantified in this study is widely used among snakes (Shine, 1991; Greene, 1997), and similar methods could be used to measure the foraging behaviors of other species. Timber Rattlesnakes exhibit general natural history characteristics that are shared among a variety of other rattlesnake species (Klauber, 1972), and it is likely that the general patterns of infrequent ambush predation on mammalian prey hold for other *Crotalus* spp. This study outlines a method that can be used to quantify foraging behavior in a wide variety of similar species, providing a means for detailed comparative studies. Interspecific and intraspecific comparisons would be valuable in elucidating the influence of foraging strategies on life history traits and population characteristics.

ACKNOWLEDGMENTS

For field assistance, I thank R. Corneau, A. Smith, and J. Cancalosi. For aid with surgical techniques, I thank H. Reinert. For financial support, I thank the Kieckhefer Adirondack Fellowship, the USDA, and the National Science Foundation (DDIG 0308919). This manuscript was greatly improved by comments from K. Rypien, K. Adler, V. Clark, and H. Greene. These experiments were approved by Cornell University's Animal Care and Use Committee (IACUC Protocol No. 99-60-03).

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