

Diet and Foraging Behaviors of Timber Rattlesnakes, *Crotalus horridus*, in Eastern Virginia

Author(s): Scott M. Goetz, Christopher E. Petersen, Robert K. Rose, John D. Kleopfer, and Alan H. Savitzky

Source: Journal of Herpetology, 50(4):520-526.

Published By: The Society for the Study of Amphibians and Reptiles

DOI: <http://dx.doi.org/10.1670/15-086>

URL: <http://www.bioone.org/doi/full/10.1670/15-086>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Diet and Foraging Behaviors of Timber Rattlesnakes, *Crotalus horridus*, in Eastern Virginia

SCOTT M. GOETZ,^{1,2} CHRISTOPHER E. PETERSEN,³ ROBERT K. ROSE,¹ JOHN D. KLEOPFER,⁴ AND ALAN H. SAVITZKY^{1,5}

¹Department of Biological Sciences, Old Dominion University, Norfolk, Virginia, USA

³Naval Facilities Engineering Command Atlantic, Norfolk, Virginia, USA

⁴Virginia Department of Game and Inland Fisheries, Charles City, Virginia, USA

ABSTRACT.—During a 17-yr telemetry study, we examined the diet and ambush behavior of a population of *Crotalus horridus* in southeastern Virginia. Forty dietary items were identified from 37 fecal samples. We documented 722 instances of snakes in an ambush posture, 61% of which were in a vertical-tree posture, as if hunting arboreal prey at the base of a tree. The most common prey items were Eastern Gray Squirrels (*Sciurus carolinensis*), which accounted for 45% of all dietary items and represented an estimated 78% of total biomass consumed by *C. horridus*. Prey was not consumed in proportion to availability, based on small mammal surveys. Our analysis provides indirect evidence that the vertical-tree foraging behavior is adopted to target arboreal Eastern Gray Squirrels. Further, we provide support for the hypothesis that *C. horridus* alters ambush behavior to forage selectively for specific prey types.

Knowledge of predator–prey relationships and related foraging behaviors is important to understanding snake evolution and can provide the basis for studying broader ecological questions (Mushinsky, 1987). The diet of predators is likely influenced by a number of interrelated factors, including habitat structure (Mullin and Mushinsky, 1995; Mullin and Cooper, 1998; Reinert et al., 2011), relative sizes of prey and predator (Shine, 1991; Arnold, 1993), prey availability (Reinert et al., 1984; Capizzi et al., 1995; Beaupre, 2008), and temporal (Santos et al., 2000; Willson et al., 2010) or geographic (Kephart, 1982; Kephart and Arnold, 1982) variation in prey species. Strategies used by predators that result in the selection of prey with specific taxonomic affinities may lead to closely linked relationships between predator and prey. If prey selection is occurring, foraging behaviors of predators are expected to correlate with movement patterns and microhabitat selection of prey; however, understanding the foraging ecology of a species requires details of both foraging behaviors and diet.

Information on the composition of snake diets has been slow to accumulate because most snakes are cryptic, solitary, and eat infrequently (Zaidan and Beaupre, 2003; Clark, 2006), and virtually all obligatorily ingest prey whole (Greene, 1997), such that no remains can be observed. As a result, the known diet of a snake species often is the compilation of anecdotal records gathered from across its distribution. Such an approach may mask the detection of interpopulation variation in diet (Rodriguez-Robles, 2002) and may be problematic when ascribing associations between diet and behaviors related to prey acquisition.

Snakes are classified as either active or sit-and-wait foragers (Schoener, 1971). Active foragers constantly move through the environment to locate prey, whereas sit-and-wait foragers ambush their prey from fixed locations; however, even sit-and-wait foragers must actively search for ambush locations. The degree to which sit-and-wait foragers actively search for ambush locations varies by species along a continuum from

those that select new ambush sites frequently, “mobile ambushers” such as *Crotalus viridis* (Reinert et al., 1984), to those that relocate to new ambush sites infrequently, such as bushmasters, *Lachesis stenophrys* (Greene and Santana, 1983). Sit-and-wait foragers may select ambush sites based on the detection of prey movements or odors (Reinert et al., 1984; Duvall and Chiszar, 1990; Theodoratus and Chiszar, 2000) or on microhabitat structure (Shine and Li-Xin, 2002; Tsairi and Bouskila, 2004). Because sit-and-wait predators rely on prey movements to initiate encounters (C. H. Greene, 1986), a premium is placed on identifying sites that are frequently used by prey species, such as the runways of small mammals or trees heavily used by arboreal species.

For sit-and-wait generalist predators, such as Timber Rattlesnakes (*Crotalus horridus*), the location of ambush sites is expected to correlate with prey selection and, therefore, with diet. *Crotalus horridus* occupy a wide variety of habitats, from high-elevation deciduous forests of the Appalachian Mountains, to lowland forests of the southeastern coastal plain, and grassland prairies of the Midwest (Conant and Collins, 1998). The diet of *C. horridus* includes mainly small mammals, but occasionally, birds also are consumed (Clark, 2002). Employing chemosensory cues to locate small mammal runways along sticks and fallen logs, *C. horridus* will lie motionless with the body coiled and the head positioned perpendicular to the runway (Reinert et al., 1984). Non-log-oriented posture facilitates catching small mammals on the open forest floor. Alternatively, *C. horridus* will coil at the base of a tree, often with the anterior portion of its body looped against the tree and its head oriented vertically (Brown and Greenberg, 1992). Interestingly, geographic variation in foraging behaviors occurs, because not all tactics are observed in all populations studied (Waldron et al., 2006; Reinert et al., 2011; Wittenberg, 2012).

We investigated the association between foraging posture and diet of *C. horridus* to better understand their natural history. During a long-term radiotelemetry study at a lowland forest site in southeastern Virginia, we frequently observed snakes ambushing at the base of live trees in the vertical-tree position described by Brown and Greenberg (1992), which led us to hypothesize that snakes adopted this posture to ambush tree squirrels. Herein, we test the prediction that vertical-tree ambush posture targets Eastern Gray Squirrels (*Sciurus caro-*

²Corresponding author. Present address: Department of Biological Sciences, Auburn University, Auburn, Alabama, USA. E-mail: goetz@auburn.edu

⁵Present address: Department of Biology, Utah State University, Logan, Utah, USA



FIG. 1. Location of study site at Naval Support Activity Hampton Road, Northwest Annex in southeastern Virginia.

linensis). To do so, we compared diet, determined through fecal analysis, to the frequency of ambush postures observed during the telemetric study of this population. In our study, a positive relationship between time spent in the vertical-tree ambush position and squirrel remains in snake feces would indicate squirrels are the target of the vertical-tree ambush position. Specifically, we assess the diet of our *C. horridus* population as it relates to foraging posture and relative prey abundance and biomass.

MATERIALS AND METHODS

Study Site.—Telemetered *C. horridus* were monitored over a 17-yr period from 1995 to 2012 at Naval Support Activity Hampton Roads, Northwest Annex (NSAHR NA; formerly Navy Security Group Activity Northwest; Fig. 1). The naval base has 982 ha of deciduous and pine forests, 40.5 ha of clearcuts, and 308 ha of cotton and soybean fields. The deciduous forests are a mixture of mesic mixed hardwood and nonriverine swamp and hardwood forests, are dominated by American beech (*Fagus grandifolia*), oaks (*Quercus* spp.), tulip poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), sweet gum (*Liquidambar styraciflua*), loblolly pine (*Pinus taeda*), American holly (*Ilex opaca*), and bald cypress (*Taxodium distichum*). The pine forests are primarily *Pinus taeda*, with occasional *L. styraciflua*, *A. rubrum*, and *I. opaca* (Tetra Tech, 2014). Clearcuts are maintained by bush-hogging and prescribed fire at approximately 10-yr intervals.

Diet Analysis.—We used fecal analyses to study the diets of 37 adult *C. horridus* (SVL > 80 cm) between 1996 and 2007. Samples were opportunistically collected when snakes were captured, handled for transmitter implantation, or other processing; other samples were obtained from snakes captured near the study site by regional wildlife officials. All samples were obtained within a radius of approximately 20 km of the study site and are presumed to represent the same population. Direct observations of predation events were not included in the dietary analyses to avoid sampling biases, for two reasons. First, we monitored snakes only during the day when the consumption of nocturnal prey species would not occur. Second, snakes require relatively longer periods of time to consume large prey species, such that observing the consumption of more quickly consumed small prey species was less likely.

Upon collection, we stored fecal samples in 70% ethanol and later dried and sorted by material (i.e., hairs, claws, claw sheaths, bones, teeth, and feathers). Fecal hair samples were prepared by repeated sonication in 80% ethanol for 2–3 min to remove attached debris. To identify hair samples, we obtained reference hairs from museum specimens maintained at Old Dominion University. The gross appearance of hair was examined for coloration, banding, and length. Medullary structure of hairs was examined in wet-mounted slides with compound light microscopy and then compared to reference samples and details from published literature (Mathiak, 1938; Williams, 1938; Debelica, 2005). We used scanning electron microscopy to compare cuticle scale patterns of hairs with reference samples and literature sources (Adorjan and Koleno-sky, 1980; Debelica, 2005) for those samples in which species identification based on medullary structure was inconclusive. The shape, size, and coloration of claws and claw sheaths were examined using a dissecting microscope and compared to museum specimens. Samples of teeth were compared to museum skulls to identify mammalian prey species. Some samples could be identified only to genus (*Peromyscus*) or, in one case, as simply mammalian. Feathers and bone fragments were too small or degraded to permit identification to species.

To estimate bird biomass, we took an average weight for each species known from previous *C. horridus* diet accounts (Clark, 2002), and weighted these averages based on numerical abundance in published literature. For those records identified only to order, we used the average weight of prey from dietary records belonging to that order. We estimated bird biomass for each species from mean adult weight values from Dunning (2008) and estimated the biomass of each mammalian species by selecting midpoint values from the weight range of adults from Wilson and Ruff (1999).

Foraging Behavior.—From 1995–2012, 54 telemetered *C. horridus* (29 males, 25 females) were actively monitored. Mean (\pm SE) snake snout–vent length (SVL) was $1,180 \pm 17.9$ mm (range = 899–1,485), and mean body mass was $1,449.6 \pm 72.9$ g (range = 460–2,749). Telemetry subjects were captured and surgically implanted with ~13-g temperature-sensitive radio transmitters (SI-2T, Holohil Systems Ltd., Carp, Ontario, Canada). Transmitters were implanted intraperitoneally under isoflurane anesthesia, according to the method of Reinert and Cundall (1982), in a laboratory at Old Dominion University. Each snake also was implanted with an AVID passive integrated transponder (PIT) tag (AVID Technology, Inc., Burlington, MA). During the active season (April to November) of 1995–2002 and 2005–2007, we radio-located snakes 5–7 times per week with a TRX-2000WR (Wildlife Materials, Murphysboro, IL) handheld receiver and Yagi



FIG. 2. *Crotalus horridus* ambush postures in Virginia; (A) non-log-oriented, (B) log-oriented, (C) vertical-tree.

directional antenna. In 2003, a portion of 2005, and between 2008 and 2012, we monitored snakes diurnally at a mean interval of once every two weeks. Snakes were not monitored in 2004. At each radiolocation, we recorded whether the snake's body was tightly coiled, loosely coiled, extended, or moving. Ambush behavior (lying in wait to attack unsuspecting prey) was strictly defined as a snake being tightly coiled and exhibiting several sharp folds of the anterior portion of the body (Reinert et al., 2011). Ambush posture was categorized as log-oriented, non-log-oriented, vertical-tree, or other. Log-oriented was defined as a snake either resting its head on, or facing (<1 m), a log (treefall) or fallen branch; non-log-oriented was recorded when the snake was situated on the forest floor and not within 1 m of, or facing, any forest structure (Fig. 2). The ambush posture was not always easily distinguished from a nonforaging and coiled individual; hence, the frequency of non-log-oriented ambushing may have been underestimated. The vertical-tree posture was recorded when a snake was either coiled at the base of a standing tree with its head oriented upward (Fig. 2) or when it faced a tree at distances less than 1 m from the base of the tree. Instances in which the snake was ambushing at the site of an object other than on a fallen log or at the base of a standing tree, such as a tree stump, were categorized as "other." When snakes were observed in the vertical-tree position, we recorded the species of tree used during ambushing activities.

Relative Abundance of Small Mammals.—We determined small mammal relative abundances with trapping results from a survey conducted at the study site in 2002 (Schwab, 2003). All habitats of the study site were surveyed (except for agricultural fields) with six 5-day trapping periods between February and August. Traps were open for a total of 38 days, resulting in 8,725 trap-nights. During each trapping period, a total of six drift fence arrays with pitfall traps were deployed, using an equal proportion of baited Sherman and snap traps. Arrays consisted of a 20-L bucket at the center of three 1-m drift fences. Fences were arranged in a Y-shape with 2-L buckets at the ends. Eastern Gray Squirrels, which were too large for Sherman or snap traps, were surveyed using 25 Tomahawk live traps, baited with cracked corn, peanut butter, or both and were set on the forest floor for a total of 673 trap nights.

RESULTS

Diet Analysis.—Large mammals with arboreal tendencies represented the majority of prey items consumed, with smaller, terrestrial mammals and birds comprising a minor fraction (Fig. 3). The 37 fecal samples yielded 40 prey items, with mammals comprising 87.5% of prey items, and birds the remaining fraction

(Table 1). Eastern Gray Squirrels were the most commonly consumed prey, representing 45% of all prey items and 78% of estimated biomass consumed. For snakes that consumed Eastern Gray Squirrels, the mean mass for 10 males and 8 females was 1,509 g, with the smallest male weighing 1,026 g (SVL = 997 mm) and female weighing 1,072 g (SVL = 1,092 mm). Two Eastern Cottontails (*Sylvilagus floridanus*) were the largest prey species consumed; both were eaten by large males (mean SVL = 1,271.5 mm, mean mass 2,036.5 g). Two samples contained unidentified mammals. In three instances, two different prey species were

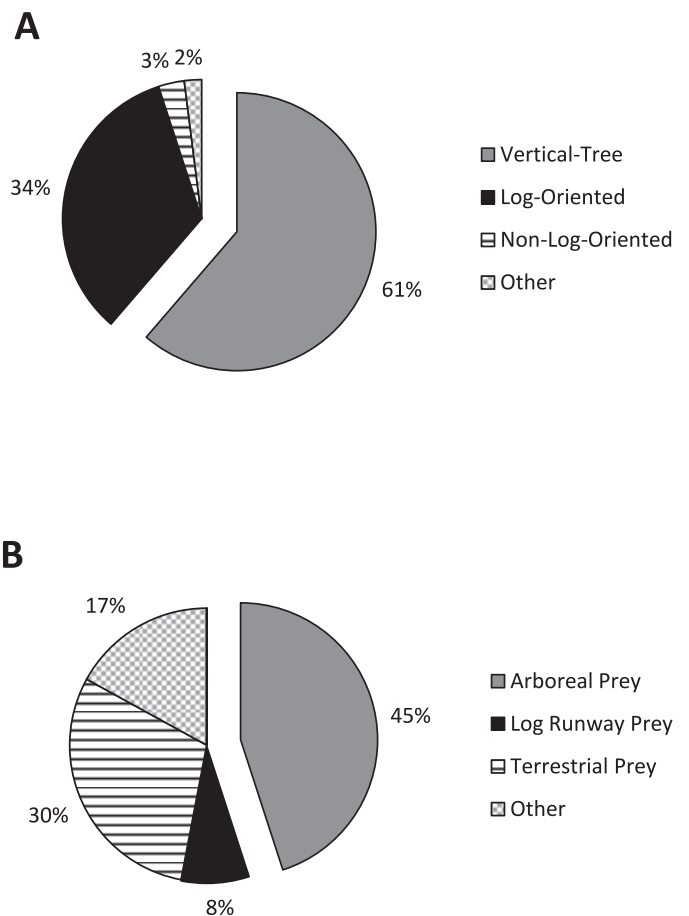


FIG. 3. Observed frequency of *Crotalus horridus* ambush posture (A) and diet composition (B) in Virginia. Prey species in diet composition were assigned to one of four categories based on location/type of most frequently used runways. The category of "Other" (B) consists of birds and unidentified mammals, which do not conform to our classification scheme.

TABLE 1. Prey species consumed by *Crotalus horridus* in southeastern Virginia, determined from fecal analysis. Individual biomass estimates are midpoint values of Wilson and Ruff (1999) for mammals and Dunning (2008) for birds. Biomass estimate for Eastern Cottontails is taken for a juvenile or small adult, assumed to be the maximum size able to be ingested by *C. horridus*.

Prey species	Number detected	Percent occurrence	Estimated individual biomass (g)	Percent of total biomass
Leporidae				
<i>Sylvilagus floridanus</i> (Eastern Cottontail)	2	5.0%	600	10.5%
Sciuridae				
<i>Sciurus carolinensis</i> (Eastern Gray Squirrel)	18	45.0%	500	78.8%
Muridae				
<i>Microtus pinetorum</i> (Pine/Woodland Vole)	1	2.5%	25	0.2%
<i>Oryzomys palustris</i> (Marsh Rice Rat)	1	2.5%	70	0.6%
<i>Sigmodon hispidus</i> (Cotton Rat)	8	20.0%	90	6.3%
<i>Peromyscus</i> spp. (White-footed Mouse)	3	7.5%	20	0.5%
Unidentified mammals	2	5.0%		
Aves (Unidentified bird spp.)	5	12.5%	68	3.0%

found in the same fecal sample (squirrel + bird; squirrel + rabbit; mouse + bird).

Foraging Behavior.—Snakes most frequently employed an ambush mode of predatory behavior, of which the vertical-tree posture was most common. During the telemetry study, 722 ambushing observations were recorded. Vertical-tree posture represented 442 (61%) of all observations (Fig. 3), and this behavior was observed equally among males (53.7%) and females (46.3%). In only 1% of vertical-tree observations was the tree dead. Snakes were observed most often (30%) at the bases of sweet gum trees, followed by oaks (16%), and loblolly pine (4%). Snakes were observed in a log-oriented posture 242 times or 33.5% of the total number of observations and in a non-log-oriented posture on 24 occasions (3%). When in the log-oriented posture, the snake was oriented to a fallen tree 15.4% and a fallen branch 18.1% of the time.

Small Mammal Abundance.—During surveys, 77 mammals representing 10 species were trapped (Table 2; Schwab, 2003). Mice (*Peromyscus* spp.) were most numerous, representing 64% of captures, and shrews (Soricidae) were second in abundance, at 25% of all captures. Although free-ranging Eastern Gray Squirrels were observed during the mammal survey, none were captured.

DISCUSSION

Prey items in feces indicated that our population of *C. horridus* consumed primarily mammalian prey, a finding consistent with other dietary studies (for review, see Clark, 2002). Occasionally birds were consumed, but even with a very conservative estimate of individual biomass, they contributed only 3% of the total biomass consumed by our snakes. Eastern Gray Squirrels,

however, constituted a much larger proportion (45%) of the diet in our study when compared to other studies. Clark's (2002) review of *C. horridus* diet, including 590 prey items from literature records and recovered from museum specimens, revealed only 17 Eastern Gray Squirrels, plus 8 remains attributed to either Fox Squirrels (*Sciurus niger*) or unknown *Sciurus*. More recently, Reinert et al. (2011) reported only three Eastern Gray Squirrels among 253 prey items from four Pennsylvania and New Jersey populations. *Crotalus horridus* dietary data combined from Clark (2002), Reinert et al. (2011), and Wittenberg (2012) indicated only 29 *Sciurus* among 884 prey items, or 3.5% of the total dietary items.

Geographic variation in dietary composition is likely given that the distribution of potential prey species vary throughout the distribution of *C. horridus*. Our knowledge of the diet of *C. horridus* is based chiefly on studies of northern populations: 750 (84%) of 884 diet records, using the north/south designations of Clark (2002). Geographic variation in dietary composition is evident, however, because prey with more northerly distributions (chipmunks, voles) occur in the diets of northern populations of *C. horridus*, whereas prey with more southerly distributions (Eastern Cottontails and Cotton Rats) are common in the diets of southern snake populations (Clark, 2002). Whether the strong selection of squirrels in our study also occurs in other southern populations of *C. horridus* remains to be determined.

We doubt that using fecal analysis to determine diet biased our sample toward larger prey, such as squirrels, that take longer to digest. Heavy-bodied, terrestrial snakes, particularly vipers, may retain feces for extended periods of time (Lillywhite et al., 2002). Retention of feces may provide a

TABLE 2. Species captured during small mammal surveys conducted at the study site in southeastern Virginia throughout 2002 (data from Schwab, 2003).

Potential prey species	Number trapped	Percent of total
Soricidae		
<i>Sorex longirostris longirostris</i> (Southeastern Shrew)	14	18.10%
<i>Cryptotis parva</i> (Least Shrew)	2	2.50%
<i>Blarina brevicauda</i> (Northern Short-Tailed Shrew)	1	1.20%
<i>Blarina carolinensis</i> (Southern Short-Tailed Shrew)	2	2.50%
Muridae		
<i>Microtus pinetorum</i> (Pine/Woodland Vole)	1	1.20%
<i>Microtus pennsylvanicus</i> (Meadow Vole)	5	6.50%
<i>Oryzomys palustris</i> (Marsh Rice Rat)	1	1.20%
<i>Sigmodon hispidus</i> (Cotton Rat)	2	2.50%
<i>Reithrodontomys humulis</i> (Eastern Harvest Mouse)	15	19.50%
<i>Peromyscus leucopus</i> (White-Footed Mouse)	34	44.20%

metabolically inert ballast, functioning to increase strike distance (Lillywhite et al., 2002). Average gut passage time of *C. horridus* is 12.8 days (Lillywhite et al., 2002), but slower feeding rates may increase passage time (Lillywhite, 2014). Snakes may accumulate feces until they reach a maximum storage threshold (Lillywhite, 2014). Therefore, we expect any bias of fecal analysis to result in finding more small prey items.

If the dietary habits of *C. horridus* in our study represent southern populations, then our results indicate a link between diet and morphology. In terms of large-bodied prey items, Clark (2002) found that *C. horridus* in southern populations consume more Eastern Cottontails, and we found frequent consumption of Eastern Gray Squirrels by the snakes of our population. Squirrels and rabbits are the largest prey items eaten by *C. horridus*, and their prevalence could be related to the larger head and body sizes and greater midbody dorsal scale counts of southern *C. horridus* when compared with northern populations (Allsteadt et al., 2006). Large body size could facilitate the specialization on large prey items (Bock, 1980) that may in turn be accompanied by shifts in foraging behavior; however, correlations between snake SVL and percent time spent either in open habitats (where densities of small prey are high) or in forested habitats (where larger but fewer prey are present) were not significant ($P > 0.05$ for both correlations). Similarly, there was no relationship between the percentage of observations of vertical-tree postures that would facilitate capture of squirrels and rattlesnake SVL ($P > 0.05$). Because we used relatively large snakes for radiotelemetry, however, we likely lacked sufficient size variation to evaluate effectively the relationship between body size, foraging behavior, and habitat.

Crotalus horridus appears to exhibit considerable individual or population-level behavioral plasticity in foraging behavior. Such variation may reflect interpopulation variation in morphology (Allsteadt et al., 2006), life-history traits (Brown, 1993), or prey communities across the species' range. Foraging behavior also may be mediated through ambush site selection in response to previous conspecific success. Clark (2007) experimentally found that *C. horridus* was more likely to select ambush sites previously used by recently fed conspecifics, rather than those of food-deprived individuals. Presumably, chemical cues left by conspecifics at ambush sites provide information on the relative profitability of the locations. Therefore, the foraging behavior of one individual could influence other members of that population despite the solitary nature of *C. horridus*. Translocating *C. horridus* between populations has revealed plasticity in foraging postures (Reinert and Rupert, 1999), and such plasticity also may occur in response to temporal changes in prey density or habitat structure.

Because sit-and-wait foragers rely on prey movements to initiate encounters, differences in snake foraging behavior may reflect differences in the movement behavior of small mammal species. Log-oriented postures may target mice and Eastern Chipmunks, which regularly use fallen trees as runways while moving through the environment (Douglass and Reinert, 1982), whereas non-log-oriented behavior seemingly targets terrestrial species, such as rabbits, shrews, rats, and voles (Douglass and Reinert, 1982). In accordance, Reinert et al. (2011) found that populations of *C. horridus* most frequently observed in a log-oriented posture consumed a higher proportion of mice and Eastern Chipmunks, whereas those most frequently observed in a non-log-oriented posture consumed a higher proportion of voles and shrews.

Our data indicate that the vertical-tree posture may be targeting arboreal mammals (Reinert et al., 2011), primarily Eastern Gray Squirrels. That posture was the one most frequently assumed by *C. horridus*, occurring in 61% of the ambushing observations. Of the arboreal prey species observed in our study, squirrels comprised 45% of food items and an estimated 79% of consumed biomass, whereas mice (*Peromyscus*; Layne, 1970; Graves et al., 1988) represented only 7.5% of prey and 0.5% of biomass. Because the vertical-tree posture would limit encounters with ground-dwelling mammals, the energetic benefits of squirrel consumption presumably are large (Clark, 2002). Beaupre (1996) estimated the annual energy budget of *C. horridus* at three times the resting metabolic rate, so that a 500-g snake would require 282 g of rodent (Zaidan and Beaupre, 2003). A single 500-g Gray Squirrel would, therefore, fulfill about two-thirds of the annual energy budget of an average (1,450 g) snake in our population.

The non-log-oriented posture was rarely observed in our population of *C. horridus*, but it nonetheless made an important contribution to overall energy acquisition. Although non-log-oriented posture comprised only 3% of all ambush observations, 30% of diet items (primarily Cotton Rats) were taken in old fields where non-log-oriented behaviors are common. We had difficulty, however, observing snakes in monocot-dominated fields (where Cotton Rats are common), such that the frequency of non-log-oriented postures likely was underestimated. Our diurnal observations of *C. horridus* also may characterize their nocturnal foraging behaviors because of the long duration, up to 67 h, spent at single ambush locations (Clark, 2006). Estimates for mean time spent by this species at an ambush location range from 7.3 h (Reinert et al., 1984) to 17 h (Clark, 2006). We could not render fine-scale time estimates from our data set, because snakes were observed only once per day; however, snakes remained at ambush sites for at least two consecutive days in 18.9% of our ambushing observations. We presume the snakes remained at ambush sites for multiple days, sleeping during the nonactivity period of their prey (Reinert et al., 1984; H. W. Greene, 1986). Therefore, diurnal observations likely are capable of capturing some, but not all, foraging behaviors targeting nocturnally active prey.

Huey and Pianka (1981) predicted that sit-and-wait predators consume prey in proportion to their abundance in the environment, although dietary composition of *C. horridus* does not always correspond to prey species density (Reinert et al., 1984, 2011). In our study, trapping biases associated with different capture probabilities of prey species (e.g., low for squirrels), and the availability of trapping data for only a single year of our multiyear telemetric study complicate the comparison of dietary composition with prey availability. The percentage of Eastern Gray Squirrels in the diet was fairly constant, however, throughout our 12-yr study. Nonetheless, tree-seed masts may cause spikes in rodent populations (Nixon et al., 1975) or may alter the rate of encounter between the snakes and their prey.

In conclusion, we observed an association between the vertical-tree ambush behavior and consumption of Eastern Gray Squirrels by *C. horridus*. When ambushing, snakes were most often observed in the vertical-tree posture, which presumably targets Eastern Gray Squirrels. Our findings add to a growing recognition that *C. horridus* is able to vary ambush and other foraging behaviors to target specific prey types, allowing for the selection of prey that best satisfies its energetic requirements within a specific habitat where the size and

density of prey vary. Our findings also highlight the need for a greater understanding of the diets of southern *C. horridus*.

Acknowledgments.—We are grateful to the US Navy for partial funding to conduct this research (cooperative agreement: N62470-95-LT-00752), access to installation property, and tremendous support of the project. We are also grateful to the Virginia Department of Game and Inland Fisheries who also partially funded this project through a State Wildlife Grant from the US Fish and Wildlife Service. At the time this research was conducted, field studies of ectotherms did not require approval by Old Dominion University's Animal Care and Use Committee. The study was permitted by Virginia Department of Game and Inland Fisheries (permit ESCP9611 and renewals). We thank V. R. Townsend Jr. for teaching us SEM techniques.

LITERATURE CITED

- ADORJAN, A. S., AND G. B. KOLENOSKY. 1980. A Manual for the Identification of Hairs of Selected Ontario Mammals. Research Report (Wildlife) No. 90. Ontario Ministry of Natural Resources, Canada.
- ALLSTEADT, J., A. H. SAVITZKY, C. E. PETERSEN, AND D. N. NAIK. 2006. Geographic variation in the morphology of *Crotalus horridus* (Serpentes: Viperidae). *Herpetological Monographs* 20:1–63.
- ARNOLD, S. J. 1993. Foraging theory and prey size-predator size relations in snakes. Pp. 87–115 in S. J. Mullin and R. A. Seigel (eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, USA.
- BEAUPRE, S. J. 1996. Field metabolic rate, water flux, and energy budgets of mottled rock rattlesnakes, *Crotalus lepidus*, from two populations. *Copeia* 1995:319–329.
- . 2008. Annual variation in time-energy allocation by timber rattlesnakes (*Crotalus horridus*) in relation to food acquisition. Pp. 111–122 in W. K. Hayes, M. D. Cardwell, K. R. Beaman, and S. P. Bush (eds.), *Biology of the Rattlesnakes*. Loma Linda University Press, CA.
- BOCK, W. J. 1980. The definition and recognition of biological adaptation. *American Zoologist* 20:217–227.
- BROWN, W. S. 1993. Biology, status, and management of the timber rattlesnake (*Crotalus horridus*): a guide for conservation. *Herpetological Circulars* 22:1–78.
- BROWN, W. S., AND D. B. GREENBERG. 1992. Vertical-tree ambush posture in *Crotalus horridus*. *Herpetological Review* 23:67.
- CAPIZZI, D., L. LUISELLI, M. CAPULA, AND L. RUGIERO. 1995. Feeding habits of a Mediterranean community of snakes in relation to prey availability. *Revue D'ecologie la Terre et la Vie* 50:353–363.
- CLARK, R. W. 2002. Diet of the timber rattlesnake, *Crotalus horridus*. *Journal of Herpetology* 36:494–499.
- . 2006. Fixed videography to study predation behavior of an ambushing foraging snake, *Crotalus horridus*. *Copeia* 2006:181–187.
- . 2007. Public information for solitary foragers: timber rattlesnakes use conspecific chemical cues to select ambush sites. *Behavioral Ecology* 18:487–490.
- CONANT, R., AND J. T. COLLINS. 1998. *A Field Guide to Reptiles & Amphibians: Eastern and Central North America*. Houghton Mifflin, USA.
- DEBELICA, A. 2005. An atlas and key to the hair of terrestrial Texas mammals. Unpubl. master's thesis. Sam Houston State University, USA.
- DOUGLASS, N. J., AND H. K. REINERT. 1982. The utilization of fallen logs as runways by small mammals. *Proceedings of the Pennsylvania Academy of Science* 56:162–164.
- DUNNING, J. B., JR. 2008. *CRC Handbook of Avian Body Masses*. 2nd ed. CRC Press, USA.
- DUVALL, D., AND D. CHISZAR. 1990. Behavioural and chemical ecology of vernal migration and pre- and poststrike predatory activity in prairie rattlesnakes: field and laboratory experiments. Pp. 539–554 in D. W. MacDonald, D. Muller-Schwarze, and S. E. Natynczuk (eds.), *Chemical Signals in Vertebrates*. Oxford University Press, UK.
- GRAVES, S., J. MALDONADO, AND J. O. WOLFF. 1988. Use of ground and arboreal microhabitats by *Peromyscus leucopus* and *Peromyscus maniculatus*. *Canadian Journal of Zoology* 66:277–278.
- GREENE, C. H. 1986. Patterns of prey selection: implications of predator foraging tactics. *American Naturalist* 128:824–839.
- GREENE, H. W. 1986. Natural history and evolutionary biology. Pp. 99–108 in M. E. Feder and G. V. Lauder (eds.), *Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates*. University of Chicago Press, USA.
- . 1997. *Snakes: The Evolution of Mystery in Nature*. University of California Press, USA.
- GREENE, H. W., AND M. SANTANA. 1983. Field studies of hunting behavior by bushmasters. *American Zoologist* 23:897.
- HUEY, R. B., AND E. R. PIANKA. 1981. Ecological consequences of foraging mode. *Ecology* 62:991–999.
- KEPHART, D. G. 1982. Microgeographic variation in the diets of garter snakes. *Oecologia* 52:287–291.
- KEPHART, D. G., AND S. J. ARNOLD. 1982. Garter snake diets in a fluctuating environment: a seven-year study. *Ecology* 1982:1232–1236.
- LAYNE, J. N. 1970. Climbing behavior of *Peromyscus floridanus* and *Peromyscus gossypinus*. *Journal of Mammalogy* 51:580–591.
- LILLYWHITE, H. B. 2014. *How Snakes Work: Structure, Function and Behavior of the World's Snakes*. Oxford University Press, USA.
- LILLYWHITE, H. B., P. DE DELVA, AND B. P. NOONAN. 2002. Patterns of gut passage time and the chronic retention of fecal mass in viperid snakes. Pp. 497–506 in G. Schuett, W. M. Höggren, M. E. Douglas, and H. W. Greene (eds.), *Biology of the Vipers*. Eagle Mountain Publishing, USA.
- MATHIAK, H. A. 1938. A key to hairs of the mammals of southern Michigan. *Journal of Wildlife Management* 2:251–268.
- MULLIN, S. J., AND R. J. COOPER. 1998. The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*)—visual stimuli facilitate location of arboreal prey. *American Midland Naturalist* 140:397–401.
- MULLIN, S. J., AND H. R. MUSHINSKY. 1995. Foraging ecology of the mangrove salt marsh snake, *Nerodia clarkii compressicauda*: effects of vegetational density. *Amphibia-Reptilia* 16:167–175.
- MUSHINSKY, H. R. 1987. Foraging ecology. Pp. 302–334 in R. A. Seigel, J. T. Collins, and S. N. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*. Macmillan Publishing, USA.
- NIXON, C. M., M. W. MCCLAIN, AND R. W. DONOHOE. 1975. Effects of hunting and mast crops on a squirrel population. *Journal of Wildlife Management* 39:1–25.
- REINERT, H. K., AND D. CUNDALL. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982:702–705.
- REINERT, H. K., AND R. R. RUPERT. 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus*. *Journal of Herpetology* 33:45–61.
- REINERT, H. K., D. CUNDALL, AND L. M. BUSHAR. 1984. Foraging behavior of the timber rattlesnake, *Crotalus horridus*. *Copeia* 1984:976–981.
- REINERT, H. K., G. A. MACGREGOR, M. ESCH, L. M. BUSHAR, AND R. T. ZAPPALORTI. 2011. Foraging ecology of timber rattlesnakes, *Crotalus horridus*. *Copeia* 2011:430–442.
- RODRÍGUEZ-ROBLES, J. A. 2002. Feeding ecology of North American gopher snakes (*Pituophis catenifer*, Colubridae). *Biological Journal of the Linnean Society* 77:165–183.
- SANTOS, X., J. GONZÁLEZ-SOLÍS, AND G. A. LLORENTE. 2000. Variation in the diet of the viperine snake *Natrix maura* in relation to prey availability. *Ecography* 2000:185–192.
- SCHOENER, T. W. 1971. Theory of feeding strategies. Pp. 369–404 in R. F. Johnston and R. A. Selander (eds.), *Annual Review of Ecology and Systematics* 2. Annual Reviews, USA.
- SCHWAB, D. 2003. Small mammal survey of six habitat types found on Naval Station Activity Northwest-Annex Chesapeake, Virginia and Currituck County, North Carolina. Technical Report, USA.
- SHINE, R. 1991. Why do larger snakes eat larger prey items? *Functional Ecology* 493–502.
- SHINE, R., AND S. LI-XIN. 2002. Arboreal ambush site selection by pit-vipers *Gloydus sheddaensis*. *Animal Behaviour* 63:565–576.
- TETRA TECH, INC. 2014. Vegetation classification and mapping at Naval Support Activity Hampton Roads-Northwest Annex, Technical Report, USA.
- THEODORATUS, D. H., AND D. CHISZAR. 2000. Habitat selection and prey odor in the foraging behavior of western rattlesnakes (*Crotalus viridis*). *Behaviour* 137:119–135.
- TSAIRI, H., AND A. BOUSKILA. 2004. Ambush site selection of a desert snake (*Echis coloratus*) at an oasis. *Herpetologica* 60:13–23.
- WALDRON, J. L., J. D. LANHAM, AND S. H. BENNETT. 2006. Using behaviorally-based seasons to investigate canebrake rattlesnake (*Crotalus horridus*) movement patterns and habitat selection. *Herpetologica* 62:389–398.

- WILLIAMS, C. S. 1938. Aids to the identification of mole and shrew hairs with general comments on hair structure and hair determination. *Journal of Wildlife Management* 2:239–250.
- WILLSON, J. D., C. T. WINNE, M. A. PILGRIM, C. S. ROMANEK, AND J. W. GIBBONS. 2010. Seasonal variation in terrestrial resource subsidies influences trophic niche width and overlap in two aquatic snake species: a stable isotope approach. *Oikos* 119:1161–1171.
- WILSON, D. E., AND S. RUFF. 1999. *The Smithsonian Book of North American Mammals*. Smithsonian Institution Press, USA.
- WITTENBERG, R. D. 2012. Foraging ecology of the timber rattlesnake (*Crotalus horridus*) in a fragmented agricultural landscape. *Herpetological Conservation and Biology* 7:449–461.
- Z Aidan, F., III, AND S. J. BEAUPRE. 2003. Effects of body mass, meal size, fast length, and temperature on specific dynamic action in the timber rattlesnake (*Crotalus horridus*). *Physiological and Biochemical Zoology* 76:447–458.

Accepted: 11 April 2016.