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Howard K. Reinert¹, Gylla A. MacGregor², Mackenzie Esch¹, Laretta M. Bushar³,
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The geographic range of the Timber Rattlesnake (*Crotalus horridus*) encompasses most of the eastern half of the United States. Although the overall diet composition of *C. horridus* has been well documented and has been reported to be very broad, local population variation has not been studied. We examined the diet and foraging behavior of *C. horridus* from four separate populations in Pennsylvania and New Jersey. A total of 253 prey items from scat samples, stomach samples, and field observation were identified to species or family level. Although voles (*Myodes gapperi*) and mice (*Peromyscus* spp.) comprised the bulk of the diet in all populations, relative prey species frequency differed significantly among the four populations. These data indicate that the food habits of *C. horridus* varied widely even within relatively small geographic distances. Comparisons with small mammal trapping data further suggest that the diet composition of this ambush predator may not simply reflect the availability of prey species. Radiotelemetric observations of *C. horridus* further indicate differing frequencies of log-oriented foraging behavior among the study sites. Analysis of body posture revealed an alternative ambush foraging posture (non-log-oriented posture) which also exhibited variation in frequency among study sites. However, selected foraging habitats at all study sites were typified by a locally high density of fallen logs and other woody debris (6% of forest-floor cover/m²). These findings indicate geographic variation in the foraging ecology of *C. horridus* and suggest behavioral plasticity in foraging response to available prey.

CLASSIC studies have demonstrated how predation moves energy and nutrients through ecosystems (Linderman, 1942), impacts population dynamics (Holling, 1959), influences community structure (Paine, 1974), and drives the evolution of both predators and prey (Fenton and Fullard, 1981). More recent research lends strong support to the contention of Hairston et al. (1960) that predation may serve as the primary force for maintaining community function and stability (Terborgh et al., 2001; Springer et al., 2003; Myers et al., 2007). Thus, understanding the structure and dynamics of ecological communities requires a thorough knowledge of the relationship between predators and their prey.

All snakes are predators, but ascertaining the role of most snake species in community trophic dynamics is hampered by several factors. Snakes, particularly viperids, feed infrequently on large prey, swallow their prey entire, and efficiently digest both soft tissue and bone (Pough and Groves, 1983; Cundall and Greene, 2000). This process leaves little evidence of foraging events and results in fecal remains that are often difficult to accurately identify. In addition, snakes often occur at low population densities, and individuals are difficult to monitor repeatedly due to their cryptic or reclusive behavior (Reinert, 1993). However, studies of invasive snake species illustrate that snakes have the potential to impact prey density and can strongly influence community structure (Savidge, 1987).

The evolutionary success of modern snakes stems largely from adaptations and extensive variation associated with feeding mechanisms (Cundall and Greene, 2000). Likewise, within snake species there is frequently broad ontogenetic (Godley, 1980; Mushinsky et al., 1982; Burghardt, 1993) and geographic (Arnold, 1977; Krause and Burghardt, 2001; Rodríguez-Robles, 2002) variation in diet composition, both of which suggest concurrent variation and plasticity in foraging behavior (Arnold, 1981; Mushinsky, 1987).

Optimal foraging theory assumes that this variation in the foraging strategies of predators is shaped by evolution to maximize net energy gain (Arnold, 1993; Perry and Pianka, 1997). Predators that maximize energy gain are generally more successful at balancing trade-offs and constraints, and make the best foraging “decisions.”

The Timber Rattlesnake (*Crotalus horridus*) is distributed across much of the eastern United States and has adapted to a variety of habitats, ranging from rocky, deciduous upland forests of the Appalachian Mountain Range to low-lying, sandy, evergreen-dominated forests of the Atlantic Coastal Plain (Ernst and Ernst, 2003). Consistent with its wide distribution, *C. horridus* displays an extensive list of consumed prey and evidence of broad-based geographic variation among populations from mountainous and lowland regions (Clark, 2002). *Crotalus horridus* is reportedly an opportunistic predator that ambushes its chiefly mammalian prey at fallen logs (Reinert et al., 1984) or at the base of trees (Brown and Greenberg, 1992). Its rather large size (total length often over 1.25 m) and wide distribution (Ernst and Ernst, 2003) combined with its unique sensory capabilities (e.g., infrared radiation detection) and prey capture mechanism (i.e., venom delivery system) make it an efficient and important forest-floor predator.

We conducted intensive, long-term studies of *C. horridus* inhabiting differing habitats at four distinct study sites. We combined traditional dietary analysis (stomach and scat contents) with behavioral observations (radiotelemetry) and assessments of prey composition (trapping and tracking) to examine variation in the relationship between a snake predator and its prey. Specifically, we asked two fundamental questions: Is the dietary composition of *C. horridus* the same among the study sites; and is the foraging behavior of *C. horridus* the same among the study sites?

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MATERIALS AND METHODS

Study areas.—We studied the diet and foraging behavior of *C. horridus* at four distinct geographic locations in Pennsylvania and southern New Jersey over 27 years: Hawk Mountain Sanctuary, Berks County, Pennsylvania (40.6°N, 75.9°W); Fort Indiantown Gap Military Reservation, Lebanon County, Pennsylvania (40.4°N, 76.6°W); Tiadaghton State Forest near Slate Run, Lycoming County, Pennsylvania (41.5°N, 77.5°W); and the Pine Barrens, Ocean County, New Jersey (39.8°N, 74.3°W). The closest study areas, Hawk Mountain (sampled from 1979–1993) and Fort Indiantown Gap (sampled from 1998–2001), were located 60 km apart along the leading ridge of the Appalachian Mountains in southeastern Pennsylvania. The two most distant study areas were located 300 km apart in the central Appalachian Mountains of Pennsylvania near Slate Run (sampled from 2002–2006), Lycoming County, and in the Pine Barrens of New Jersey (sampled from 1996–2004). The foraging habitats at Hawk Mountain, Fort Indiantown Gap, and Slate Run consisted of similar deciduous, hardwood forests dominated by various species of oak (*Quercus* spp.), while the Pine Barrens habitat of the Atlantic Coastal Plain was dominated by Pitch Pine (*Pinus rigida*). Reinert (1984, 1993), Reinert and Zappalorti (1988), MacGregor (1999), and Reinert et al. (2011) provide more detailed descriptions of these habitats.

Diet determination.—Scats, stomach contents, and foraging observations from captured and radio-tracked snakes in each population were opportunistically collected between 1979 and 2006. Snakes were not palpated to retrieve food contents. Whenever possible, we recorded information pertaining to sex, color variation, mass, total length, head length, and tail length. We preserved all dietary samples in 70% ethanol and later examined them under a dissecting microscope (10X magnification) for teeth, nails, and bone fragments. We compared any teeth and/or jawbones present in the sample with museum-prepared skulls of potential prey species collected from the study sites. We examined hair for macroscopic traits such as length, color, and banding pattern. Wet-mount slides were prepared for compound light microscopic examination (300X magnification) of the medullar pigmentation of the hairs. Reverse impression slides of cuticle scale patterns were made by pressing hairs into partially dry, clear nail polish spread on glass microscope slides. We compared the characteristics from both wet-mount and reverse impression slides with reference hairs taken from study skins of potential prey and with mammal hair keys (Mathiak, 1938; Williams, 1938; Adorjan and Kolenosky, 1969). Nails were compared with those from study skins for qualities such as size, shape, and, in some instances, the manner in which they attached to the toe. Prey were identified to the lowest taxonomic level possible. Two sympatric species of mice (White-footed Mouse, *Peromyscus leucopus*, and Deer Mouse, *Peromyscus maniculatus*) were found to be indistinguishable in prey remains and were grouped together (*Peromyscus* spp.). Depending upon the remains available, it was sometimes difficult to distinguish among several species of voles belonging to the subfamily Arvicolinae, such as *Myodes gapperi*, *Microtus pennsylvanicus*, and *Microtus pinetorum*. In such cases we identified the prey as “arvicoline” for data analysis. Because of their low frequency of occurrence in the diet samples, squirrels and chipmunks (i.e., *Glaucomys*

sabrinus, *Tamias striatus*, *Tamasciurus hudsonicus*, *Sciurus carolinensis*) as well as shrews (*Sorex* spp. and *Blarina brevicauda*) were grouped by family (Sciuridae and Soricidae, respectively) for most analyses.

Prey abundance.—We followed standard small mammal sampling procedures in an effort to assess the apparent, relative abundance of prey at each study location (Wilson et al., 1996). We established live-trapping grids using 7.6 cm × 8.9 cm × 23 cm Sherman live traps (H. B. Sherman Traps, Tallahassee, FL), transects of snap-traps (Woodstream Corporation, Lititz, PA) and/or pitfall traps for small mammals during the same time period that diet samples were collected from snakes. Baited traps contained a 1:1 mixture of peanut butter and rolled oats. The information regarding small mammal diversity and density was collected over a 27-year period, and on several occasions these data were collected in collaboration with researchers working on other projects. Consequently, there were differences in sampling methods and intensity at the various study sites.

Seven trapping grids were established in both forested and open habitat used by *C. horridus* at Hawk Mountain. Each of these 0.15 ha grids contained 24 live traps spaced at 10-m intervals. The trapping provided 1,194 trap nights of sampling efforts.

At Indiantown Gap, trapping transects consisting of 25 randomly placed stations each with 2–4 snap-traps/station were placed at 17 separate locations in a variety of forested and open habitats within the study area. The traps were placed in small mammal runways or along natural corridors of travel such as logs or rocks. At each of the 17 sampling sites, a variable number of pitfall traps (Wilson et al., 1996) were also used to facilitate the capture of smaller species such as shrews. This resulted in 4,350 trap nights of sampling effort.

We established six separate 0.625 ha trap grids each containing 36 live traps set at 5-m intervals at the Slate Run study site. These trap grids were placed mainly in forested habitat known to be utilized by foraging rattlesnakes (based upon capture and telemetry information). The same six trapping grids were operated periodically over six consecutive years, resulting in 5,273 trap nights of sampling effort.

In the Pine Barrens, a variety of trapping grids and methods were used in forested and associated wetland habitat utilized by *C. horridus*. Primarily, data were obtained from 12 grids (0.25 ha area) containing 36 live traps set at 10-m intervals and two smaller grids (0.12 ha area) containing 20 traps. In addition, six live traps placed in a 10-m diameter circular pattern (0.008 ha area) were set in the immediate vicinity of foraging snakes (MacGregor, 1999). At these sampling sites, one trap circle was centered on the position of a foraging snake and a replicate trap circle was placed a distance of 15–30 m from the snake. These trapping programs resulted in 4,312 trap nights of sampling effort.

For comparison with dietary data, we combined the trapped mammal species into the following broader groups: *Peromyscus* spp. (*P. leucopus* and *P. maniculatus*), arvicoline rodents (voles), Sciuridae (squirrels), and Soricidae (shrews). The apparent, relative abundance of trapped species was calculated on the basis of catch/unit effort (ignoring recaptured individuals), where one trap set for one night was equivalent to one trap-night of effort.

Mammals found dead in traps were used as reference specimens for comparison with diet samples. We derived

mass estimates of prey from the average mass of trapped specimens. Estimated masses of species found in the diet but not trapped (*Zapus hudsonicus*, *Sylvilagus floridanus*, and *Sciurus carolinensis*) were taken from Merritt (1987).

Behavior.—Radiotelemetric tracking of 198 snakes (Hawk Mountain, $n = 71$; Indiantown Gap, $n = 14$; Slate Run, $n = 67$; Pine Barrens, $n = 46$) occurred in the four populations for periods of 2–6 years. We surgically implanted transmitters (representing less than 3% of body mass) following Reinert and Cundall (1982) and Reinert (1992). We located monitored snakes an average of once every 48 hours. At most locations we recorded the behavior and body posture of the snake and, in many cases, photographs were taken. We also noted the presence of an obvious food bolus, impending defecation, and/or molting condition. Based upon this information, we classified the behavior of a snake into one of the following categories: 1) traveling—moving across the ground surface or in an arrested crawl; 2) exposed/inactive—visible, coiled to loosely looped posture (not moving or in arrested crawl); 3) hunting—coiled at a fallen log in foraging posture as described by Reinert et al. (1984) or as later described in this report; or 4) concealed—not visible, under surface rock or debris. Observations were not used in analyses when the behavior and body posture were ambiguous. Photographs, digital images, and field drawings of snakes in foraging postures ($n = 453$) were used to analyze body posture. The distance from the tip of snout to the center of discernable prey runways was measured for a sample of snakes in foraging postures not associated with fallen logs ($n = 30$).

Habitat.—The percent fallen log or coarse woody debris (CWD) cover in a 1-m² sampling plot centered on the location of foraging snakes was determined using photographic/digital image analysis (Reinert, 1984). For comparison to the sites selected by foraging snakes, the CWD cover was assessed at 100–150 random forest-floor sites at each study area.

Statistical analysis.—Comparisons of group frequencies were performed as $R \times C$ Chi-square contingency tables (Zar, 1996). The observed frequency of prey species ingested at each study site was compared among all locations with a 4×4 Chi-square contingency table where rows represented locations and columns represented prey species groups (*Peromyscus* spp., arvicoline rodents, Scuridae, and Soricidae). We performed most location to location comparisons in the same manner as either 2×4 or 2×3 tables (by combining Scuridae and Soricidae) depending on the size of groups and expected frequencies. However, two location comparisons (Indiantown Gap to Slate Run and Indiantown Gap to Pine Barrens) were performed as 2×4 Fisher's Exact Tests (Freeman and Halton, 1951) due to the small frequencies in several prey categories. The observed frequency of prey species ingested at each study site was also compared with the frequency of potential prey species trapped at each site with 2×4 or 2×3 tables, where rows represented trapped and ingested categories and columns represented prey species. Similar Chi-square contingency tables were used to compare the diet composition of males to females, and "yellow variation" snakes to "black variation" snakes (Conant and Collins, 1998). We used Pearson product-moment correlations (Sokal and Rohlf,

1995) to assess the relationships between the estimated mass of consumed prey and the total length, head length, and mass of snakes. One-way ANOVA (Model I) was used to compare the morphological characteristics of snakes and to compare the CWD cover among the different sampling locations. Prior to ANOVA, a modification of Levene's tests for homogeneity of variances (Brown and Forsythe, 1974) was performed. For all ANOVA results the assumptions of normality and homogeneity of variances were accepted. Chi-squared analyses were performed using VassarStats (<http://faculty.vassar.edu/lowry/VassarStats.html>). All other statistical analyses were performed using Statistica (Version 8.0, StatSoft, Inc., Tulsa, OK).

We assessed prey selectivity using an index based upon the foraging ratio derived from diet composition and the apparent prey availability from trapping data (Manly et al., 1993). We calculated group selection indices, their 95% confidence intervals, and tests of random prey selectivity according to Krebs (1999) using Programs for Ecological Methodology, second edition (Version 6.1.1, Exeter Software, East Setauket, NY).

RESULTS

Dietary divergence.—A total of 253 prey items were identified from the scat or stomach contents of 194 snakes (Table 1). Overall, the populations of *C. horridus* exhibited significant differences in the proportion of small mammals contained in their diets ($\chi^2_9 = 90.94$, $P < 0.001$; Fig. 1). Populations differed significantly from one another in their diet composition with the exception of Indiantown Gap and Slate Run and Indiantown Gap and the Pine Barrens (Table 2). In the Hawk Mountain population, *Peromyscus* spp. was the dominant prey item of *C. horridus*, while in the other three populations arvicoline rodents were consumed at twice the frequency of *Peromyscus* spp. Shrews (*Sorex cinereus*) represented 19.3% of the diet of snakes in the Pine Barrens, but less than 4% at Slate Run and Hawk Mountain. Similarly, sciurids (*G. sabrinus*, *T. hudsonicus*, *T. striatus*) comprised 18.0% of the diet at Slate Run, but less than 6% in the remaining populations.

Dietary divergence among populations could not be attributed to differences in the sizes of the snakes sampled (Table 3). Analysis of variance indicated that snakes from the four sampled populations were similar in total length ($F_{3,175} = 2.74$, $P = 0.05$), head length ($F_{3,161} = 1.91$, $P = 0.13$), and mass ($F_{3,151} = 0.60$, $P = 0.62$). Likewise, the estimated mean mass of ingested prey did not differ significantly among populations ($F_{3,175} = 1.51$, $P = 0.21$). Data from 84 male snakes and 91 female snakes indicated that sex did not significantly influence prey selection in the overall sample ($\chi^2_3 = 4.75$, $P = 0.19$). Similarly, data from 78 "black variation" snakes and 88 "yellow variation" snakes indicated that body coloration had no obvious influence on prey selection in the overall sample ($\chi^2_3 = 1.81$, $P = 0.61$).

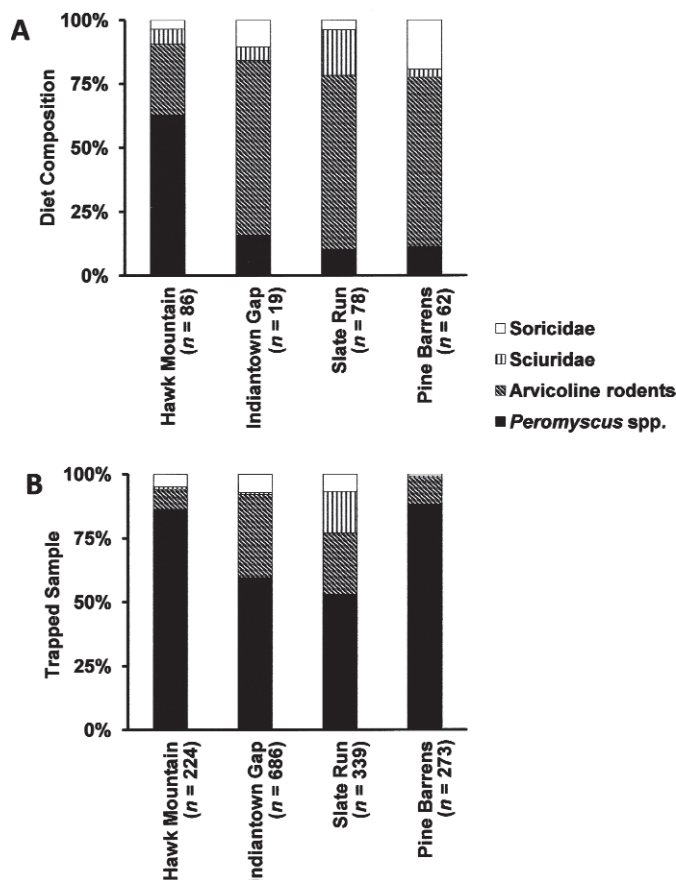
Examination of the overall sample of snakes having known prey items ($n = 162$) indicated that there were no strong correlations between estimated prey mass and snake total length ($r = 0.113$, $P = 0.15$), head length ($r = 0.142$, $P = 0.07$), or snake mass ($r = 0.154$, $P = 0.05$). Although larger snakes tended to add larger prey items (e.g., *S. carolinensis* and *T. hudsonicus*) to their diet, they also continued to eat small prey (especially *Peromyscus* spp. and arvicoline rodents) with high frequency (Fig. 2). For

Table 1. Prey Species Consumed by *Crotalus horridus* from Four Study Areas in Pennsylvania (PA) and New Jersey (NJ) Determined from Scat Samples and Stomach Contents.

Prey species identified	Hawk Mountain, PA	Indiantown Gap, PA	Slate Run, PA	Pine Barrens, NJ
<i>Blarina brevicauda</i> (Short-tailed Shrew)	0	0	1	0
<i>Sorex cinereus</i> (Masked Shrew)	3	2	2	12
<i>Sylvilagus floridanus</i> (Cottontail Rabbit)	1	0	0	0
<i>Zapus hudsonicus</i> (Jumping Mouse)	1	0	0	0
<i>Myodes gapperi</i> (Red-backed Vole)	19	7	17	29
<i>Microtus pennsylvanicus</i> (Meadow Vole)	1	4	1	4
<i>Microtus pinetorum</i> (Pine Vole)	0	2	0	4
Arvicoline (undetermined vole spp.)	4	0	35	4
<i>Peromyscus leucopus</i> / <i>P. maniculatus</i> (White-footed/Deer Mouse)	54	3	8	7
<i>Glaucomys sabrinus</i> (Flying Squirrel)	0	0	4	0
<i>Sciurus carolinensis</i> (Gray Squirrel)	2	0	0	1
<i>Tamiasciurus hudsonicus</i> (Red Squirrel)	0	0	2	1
<i>Tamias striatus</i> (Chipmunk)	3	1	8	0
Aves (unidentified bird spp.)	4	0	1	0
<i>Lymantria dispar</i> (Gypsy Moth pupa)	1	0	0	0
Total number of prey items	93	19	79	62
Number of snakes sampled	64	17	63	50

example, a scat from a 1826-g male Pine Barrens snake had remains of a Masked Shrew (*S. cinereus*) with an estimated mass of 4.5 g (0.25% of snake mass). The largest prey items ingested were Gray Squirrels (*S. carolinensis*) estimated at

just over 340 g that were eaten by a 650-g snake (52.3% of snake mass) and a 1275-g snake (26.7% of snake mass) at Hawk Mountain.

**Fig. 1.** Diet composition from scat and stomach samples (A) for *Crotalus horridus* and the apparent, relative prey availability based upon trapping samples (B) at the four study sites.

Prey abundance and consumption.—A total of 1,522 small mammals from the four prey categories were trapped in 15,129 trap-nights at the four study areas. *Peromyscus* spp. (represented predominantly by *P. leucopus* at all sites) was the most frequently trapped species and accounted for 67% of all captures. Arvicoline rodents (represented predominantly by *M. gapperi* at all sites) accounted for 23% of all captures. However, the apparent abundance of the various prey groups (Table 4) and the proportional composition of the potential prey species trapped (Fig. 1) differed significantly among the four study areas ($\chi^2_9 = 274.37$, $P < 0.001$).

Chi-square analyses indicated that, for every population, the frequency of prey species ingested by snakes also differed significantly from the frequency of small mammals trapped in the shared habitat (Hawk Mountain: $\chi^2_2 = 23.04$, $P < 0.001$; Indiantown Gap: $\chi^2_2 = 14.78$, $P < 0.001$; Slate Run: $\chi^2_3 = 65.10$, $P < 0.001$; Pine Barrens: $\chi^2_2 = 158.96$, $P < 0.001$; Fig. 1). In all populations, *Peromyscus* spp. was consumed less frequently and arvicoline rodents were consumed more frequently than predicted by prey selectivity analysis (Table 5).

Foraging behavior.—Radiotracking of 198 snakes resulted in a total of 3,560 categorized observations of rattlesnake behavior at the four study areas. The frequency of observation of the four behavioral categories differed significantly among the sites ($\chi^2_9 = 649.59$, $P < 0.001$). The most obvious difference in these data was the great disparity in the frequency of observation of the typical hunting posture among the populations (Fig. 3). The previously described log-oriented foraging posture of Reinert et al. (1984) was observed with high frequency at Hawk Mountain (220 of 836 observations), occasionally observed at Slate Run (43 of 902 observations), rarely observed at Indiantown Gap (nine of 303 observations),

Table 2. Statistical Comparisons of the Proportion of Small Mammals in the Diet of *Crotalus horridus* from Four Populations in Pennsylvania (PA) and New Jersey (NJ). ** $P < 0.01$; *** $P < 0.001$; †Fisher's exact 2-tailed P .

Population	Hawk Mountain, PA	Indiantown Gap, PA	Slate Run, PA
Indiantown Gap, PA	$\chi^2_2 = 14.21^{***}$		
Slate Run, PA	$\chi^2_2 = 48.05^{***}$	$P = 0.29^\dagger$	
Pine Barrens, NJ	$\chi^2_2 = 39.44^{***}$	$P = 0.75^\dagger$	$\chi^2_3 = 15.36^{**}$

and rarely observed in the Pine Barrens (three of 1,519 observations). This suggests that alternative foraging strategies were used in differing frequencies at each site.

The log-oriented foraging posture was easily recognized (Fig. 4A and Reinert et al., 1984:fig. 1). Analysis of field drawings, photographs, and digital images ($n = 155$) of snakes in this position indicated a consistent pattern of body posture comprised of a series of two compact loops consisting of seven acute changes in body direction within the anterior half of the body. The remaining portion of the body was coiled tightly with the head extending past the outermost coil and with the chin of the snake resting on, or oriented directly toward, the log (Fig. 4A).

Beginning in 1996, our observations of *C. horridus* in the Pine Barrens indicated that this same foraging posture was also frequently assumed by snakes coiled in forest-floor litter away from fallen logs (Fig. 4B). A comparative analysis of snake body positions from field drawings, photographs, and digital images ($n = 298$) revealed that, except for the absence of a log, all other characteristics of both postures were nearly identical. Furthermore, this non-log-oriented foraging posture could be easily separated from resting postures assumed by pre-molt, post-ingestive, and basking snakes that were not suspected to be foraging. In resting postures associated with these conditions, the body was typically arranged in a loose coil or elongated loop, the neck was straight, the head was positioned inside the outer-most body loop, and there were normally only three acute directional changes within the anterior half of the body (Fig. 4E, F).

Schematic outlines illustrate the typical position of the anterior portion of a snake's body in both the log-oriented foraging posture (Fig. 4C: schematic of the snake in Fig. 4A) and the non-log-oriented foraging posture (Fig. 4D: schematic of the snake in Fig. 4B). Comparative schematic outlines of snakes in non-foraging postures (Fig. 4G, H: schematics of the snakes in Fig. 4E, F, respectively) illustrate the reduced number of directional body changes and difference in the orientation of the head and neck.

To facilitate comparison, all of the foraging postures illustrated have the first directional body change (at the neck) turning toward the right. Based upon 48 field photographs and digital images, the posture was equally likely to be assumed in the reverse direction (28 left to 20

right; $\chi^2_1 = 1.02$, $P = 0.31$). However, for six snakes having two repetitive photographic samples, the direction of the coils was consistent in both, suggesting the possibility that individual snakes may exhibit a preferred postural direction.

Following its identification as a foraging behavior, the non-log-oriented foraging posture was recorded in 26.6% of the observations in the Pine Barrens (157 of 590 observations in 1997–1998), 19.8% of the observations (60 of 303 observations) at Indiantown Gap, and 5.2% of the observations at Slate Run (47 of 902 observations; Fig. 5). Because the identifying cues of this position are more subtle than the unambiguous, log-oriented foraging posture, it is probable that these frequencies underestimated the actual occurrence of this behavior. At all four study sites, individual snakes were observed to use both the log-oriented and non-log-oriented postures in their foraging activity at different times. The relative frequency of both behaviors could not be determined for the Hawk Mountain population because the non-log-oriented posture was not clearly identified until after sampling at this site was completed. However, archived images revealed that snakes at Hawk Mountain also demonstrated the non-log-oriented foraging posture.

Signs of small mammal activity could often be discerned adjacent to snakes observed in the non-log-oriented posture. Well-traveled, small mammal runways were frequently identifiable as furrows in the surface litter or soil directly in front of these snakes. In areas of thick surface vegetation, snakes were sometimes observed to position themselves adjacent to larger, more obvious animal trails (typical "game" trails containing the tracks of deer, foxes, and raccoons). Where clearly discernable runways or trails were evident, the distance from the snout of the snake to center of the runway averaged 3.2 cm (SE = 0.41, $n = 30$). An adult female snake that was observed in the described posture at the intersection of two well-worn pathways had an obvious stomach bolus the following day. Several snakes were observed in this posture less than 0.5 m from small mammal burrows. In several cases the presence of these burrows was identified through live trapping and fluorescent dye tracking of mice (MacGregor, 1999). In addition, all snakes monitored in the Pine Barrens in 1997–1998 ($n = 12$) were observed to assume this posture when in close proximity to "shuck" piles. Shuck piles consisted of large (often 1 m in

Table 3. Morphological Characteristics (Mean \pm SE and n in Parentheses) of Snakes (*Crotalus horridus*) Used To Determine Diet Composition from Four Populations in Pennsylvania (PA) and New Jersey (NJ).

Population	Total length (cm)	Head length (cm)	Mass (g)
Hawk Mountain, PA	97.5 \pm 1.84 (63)	4.17 \pm 0.062 (63)	649.7 \pm 39.11 (53)
Indiantown Gap, PA	87.4 \pm 4.20 (14)	3.91 \pm 0.15 (14)	579.9 \pm 81.11 (14)
Slate Run, PA	90.4 \pm 2.32 (63)	3.98 \pm 0.08 (63)	644.1 \pm 45.76 (62)
Pine Barrens, NJ	94.7 \pm 2.56 (39)	3.92 \pm 0.10 (25)	558.4 \pm 71.95 (26)

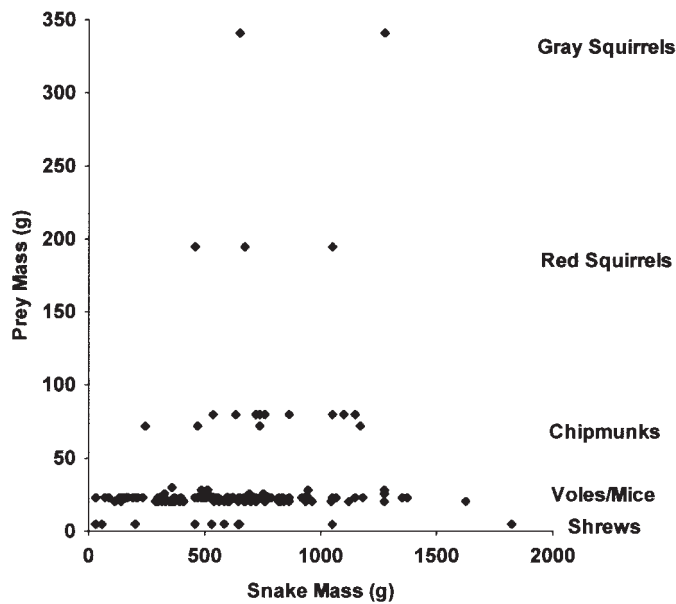


Fig. 2. Body mass of 162 individuals of *Crotalus horridus* and estimated mass of prey items in their scat or stomach samples.

diameter) masses of debris left at sites where rodents or squirrels repeatedly stripped the scales from the central stem of pine cones (*P. rigida*) to get to the seeds.

As with the log-oriented posture, our observations suggested that snakes may have held the non-log-oriented posture at the same location through a 24-hour period. On a small number of occasions ($n = 15$) in the Pine Barrens, snakes remained apparently stationary in this position for more than 48 hours until a meal was obtained. For example, a juvenile male was observed in the same posture at the same location on each of four successive days before obtaining a meal of a PIT-tagged mouse (*P. leucopus*). After digestion and subsequent molting, this snake returned to precisely the same foraging spot and obtained a second meal within two days (another PIT-tagged *P. leucopus*). An adult female made a series of three short moves (less than 2 m), staying in each location for two days. At every location this snake assumed the described posture. At the third location it obtained a meal (obvious food bolus).

Habitat structure.—The percent CWD cover at 553 randomly selected forest locations was similar among the three Appalachian Mountain sites but significantly lower in the Coastal Plain Pine Barrens ($F_{3,549} = 8.75, P < 0.001$). Typically, the forest floor in the oak-dominated mountain study areas averaged 3.4% CWD cover (SE = 0.40, $n = 453$), while the pine-dominated Coastal Plain forest averaged only 0.8% CWD cover (SE = 0.26, $n = 100$). However, the actual

foraging sites selected by snakes within each habitat did not differ in the amount of CWD cover ($F_{3,492} = 2.47, P = 0.06$), averaging 6% CWD cover (SE = 0.46, $n = 496$) at all of the study sites.

DISCUSSION

The prey items found in this study indicate that small mammals comprised the vast majority of the diet of *C. horridus* in all four populations examined. This result is consistent with those published in previous dietary studies of this species (reviewed in Clark, 2002). Our findings also indicate the occurrence of significant interpopulation variation in the dietary composition of *C. horridus* over rather small geographic distances. Uhler et al. (1939), Savage (1967), Reinert et al. (1984), and Clark (2002) found *Peromyscus* spp. to be a principal prey species, as was the case for our Hawk Mountain population. In contrast, Surface (1906) and Keenlyne (1972) identified arvicoline rodents as the primary prey species, which is consistent with our data from Indiantown Gap, Slate Run, and the Pine Barrens. Two populations of *Crotalus lepidus* separated by only 40 km but differing greatly in elevation (476 m) exhibited substantially divergent diets as a consequence of thermal constraints which resulted in pronounced differences in foraging behavior (Beaupre, 1995a, 1995b). In contrast, *Sistrurus catenatus edwardsii* from three widely separate populations (greater than 600 km) exhibited little dietary divergence, while the three subspecies of *S. catenatus* sampled from across the species’ broad geographic range showed extensive dietary differences related to morphological, behavioral, and habitat variation (Holycross and Mackessy, 2002). It is unlikely that the observed dietary variation in our samples of *C. horridus* was linked to variation in thermal environments. However, site variation in habitat structure, prey population density, and foraging behavior may have all contributed to the observed differences.

Crotalus horridus continued to eat small mammalian prey items even after growing rather large, accounting for the lack of a strong correlation between prey size and snake size. Smaller snakes are restricted by their gape size when selecting prey (King, 2002) and must limit their diet to smaller prey choices such as shrews and mice. As *C. horridus* increases in size, the concurrent increase in gape size allows them to include larger prey such as squirrels and rabbits (Clark, 2002). However, the continued inclusion of small prey results in an “ontogenetic telescope” instead of an ontogenetic shift in the relationship between prey size and snake size (Arnold, 1993). As a sit-and-wait predator, *C. horridus* expends little energy when foraging for food, so smaller prey items are not energetically unfavorable to ingest (Zaidan and Beaupre, 2003).

Table 4. Apparent Abundance of Potential Prey Species for *Crotalus horridus* in Samples of Trapped Mammals at Four Locations in Pennsylvania (PA) and New Jersey (NJ).

Study area	Total number of trap-nights	Catch/100 trap-nights			
		<i>Peromyscus</i> spp.	Arvicoline	Sciuridae	Soricidae
Hawk Mountain, PA	1194	16.08	1.51	0.25	0.92
Indiantown Gap, PA	4350	9.38	5.15	0.11	1.03
Slate Run, PA	5273	3.41	1.54	1.04	0.44
Pine Barrens, NJ	4312	5.59	0.65	0.05	0.05

Table 5. Prey Selectivity of *Crotalus horridus* from Four Populations in Pennsylvania (PA) and New Jersey (NJ). Values having a negative (–) superscript indicate selection against the prey type, values with a positive (+) superscript indicate selection for the prey type, values lacking a superscript indicate no significant selectivity ($***P < 0.001$).

Population	Selection index with 95% confidence interval for				Test of random selectivity
	<i>Peromyscus</i> spp.	Arvicoline	Sciuridae	Soricidae	
Hawk Mountain, PA	0.73 [–] 0.57–0.89	3.47 ⁺ 1.00–5.94	4.34 0.00–12.14	0.71 0.00–1.84	$\chi^2_3 = 24.68^{***}$
Indiantown Gap, PA	0.26 [–] 0.01–0.61	2.08 ⁺ 1.22–2.94	7.18 0.00–26.38	1.60 0.00–4.32	$\chi^2_3 = 16.39^{***}$
Slate Run, PA	0.19 [–] 0.03–0.36	2.84 ⁺ 1.96–3.73	1.11 0.35–1.86	0.57 0.00–1.42	$\chi^2_3 = 67.68^{***}$
Pine Barrens, NJ	0.13 [–] 0.01–0.24	6.45 ⁺ 3.21–9.68	4.40 0.00–15.29	26.42 0.00–75.96	$\chi^2_3 = 146.97^{***}$

Comparisons between our small mammal trapping results and the diet composition suggest that *C. horridus* was not consuming prey items in similar proportions to their occurrence in the shared habitat. Rather, the snakes in all populations appeared to consume arvicoline rodents in a higher proportion than expected. This finding differs from the previous results of Reinert et al. (1984) who reported the diet composition of *C. horridus* at Hawk Mountain to be similar to live trapping samples. Likewise, this finding is contrary to the theoretical notion that ambush predators should be non-selective and thus consume prey in equal frequency to availability (Huey and Pianka, 1981). This lack of continuity between trapping samples and diet samples could arise in several ways.

Under laboratory conditions, *C. horridus* chose foraging locations that exhibited the chemical cues left by prey species they had previously encountered, or by successfully foraging conspecifics (Clark, 2004, 2007). The dietary experience of neonatal Garter Snakes (*Thamnophis sirtalis*) has also been shown to influence foraging behavior and, potentially, adult dietary preferences (Krause and Burghardt, 2001). Consequently, a preference for a “fluctuating” prey species (e.g., arvicoline rodents) could continue for an

extended time period even when the abundance of that prey species declines. Such intrinsic factors could be an underlying cause for the observed geographic variation in the diet and foraging behavior of *C. horridus*, as well as the differences between the observed diet and trapped prey samples.

Peromyscus spp. and arvicoline rodents may not be equally catchable by snakes due to differences in the behavior and activity levels of these rodents. For Barn Owls (*Tyto alba*), the number of predatory attempts and the pursuit time was approximately double for *P. leucopus* as compared to the arvicoline, *M. pennsylvanicus*, and the probability of capturing *M. pennsylvanicus* was nearly twice that of *P. leucopus* despite their equal frequency of occurrence in an artificial environment (Derting and Cranford, 1989). Observations suggested that differences in movement patterns and activity levels of rodents can be highly influential in eliciting differential predation rates by raptors (Glickman and Morrison, 1969; Derting and Cranford, 1989), and the same may hold true for rattlesnakes. In addition, *M. gapperi*, the arvicoline rodent most frequently consumed by *C. horridus*, is known to be active during both the day and night during the summer (Merritt, 1981), while *P. leucopus* and *P. maniculatus* remain predominantly nocturnal (Bruseo and Barry, 1995). This behavioral difference may result in a higher than expected encounter rate between *C. horridus* and *M. gapperi*. *Peromyscus* spp. demonstrates more extensive arboreal activity than most arvicoline rodents (Getz and Ginzberg, 1968; Lackey et al., 1985), which may serve to lower its contact with terrestrially foraging *C. horridus*. *Crotalus horridus* does occasionally ascend trees and bushes (Saenz et al., 1996; Coupe, 2001; Sajdak and Bartz, 2004) and has been observed foraging at the base of trees in New York in a “vertical-tree” foraging posture (Brown and Greenburg, 1992). Such behavior could increase the probability of encountering and consuming both *Peromyscus* spp. and sciurids. Unfortunately, comparative information on the dietary composition of the New York population is lacking. However, the “vertical-tree” foraging posture was not observed at any of our study locations suggesting another example of geographic variation in the foraging mode of *C. horridus*.

Several studies have demonstrated that trap type, trap placement, and community composition can incur bias with respect to the capture rate of different mammal species (Myton, 1974; Laudenslayer and Fargo, 1997; Anthony

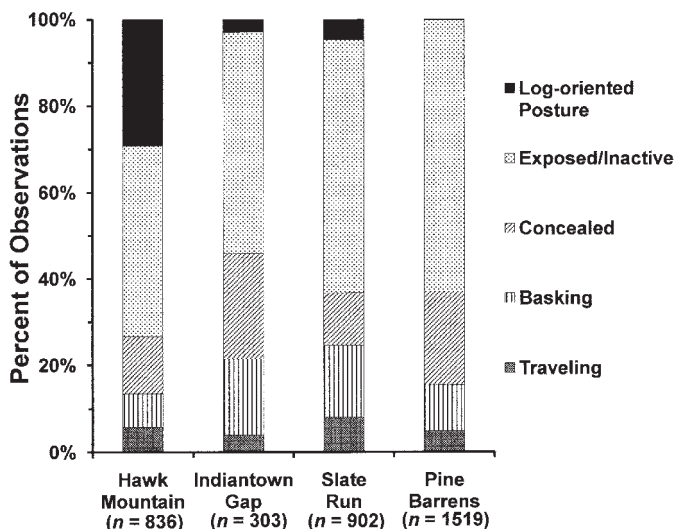


Fig. 3. Frequency of observed behaviors of radiotracked individuals of *Crotalus horridus* in four separate populations. Sample sizes (n) represent the number of observations of radiotracked animals.

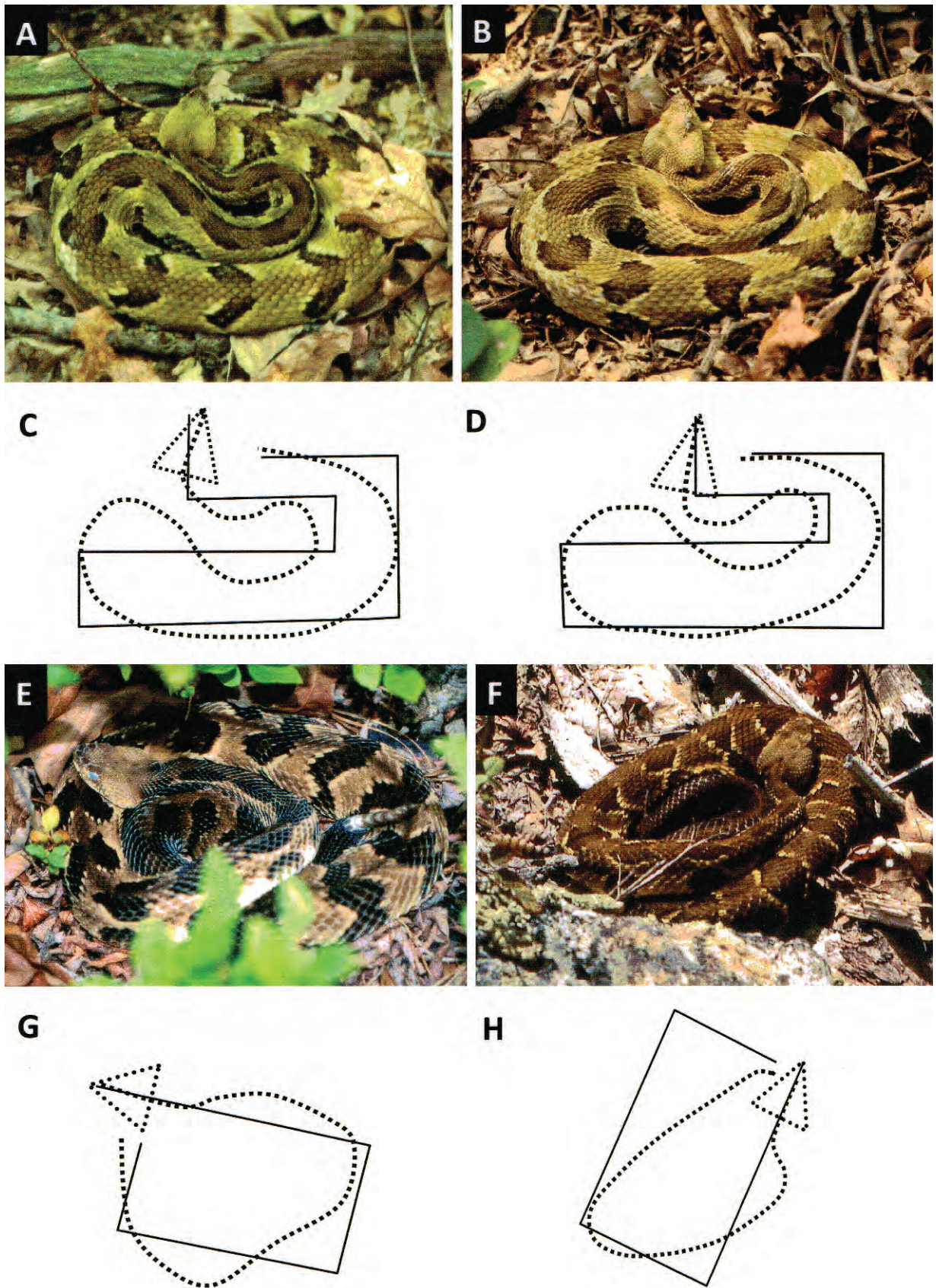


Fig. 4. Foraging and non-foraging postures in *Crotalus horridus*. Log-oriented (A), non-log-oriented (B), and schematic outlines of log-oriented (C) and non-log oriented (D) foraging postures illustrating the similarity in body position in two different snakes. Non-foraging postures of a pre-molt (E) and gravid (F) snake followed by schematic outlines of both postures (G and H). Lines in schematic diagrams indicate the number of coils and directional changes in the anterior body.

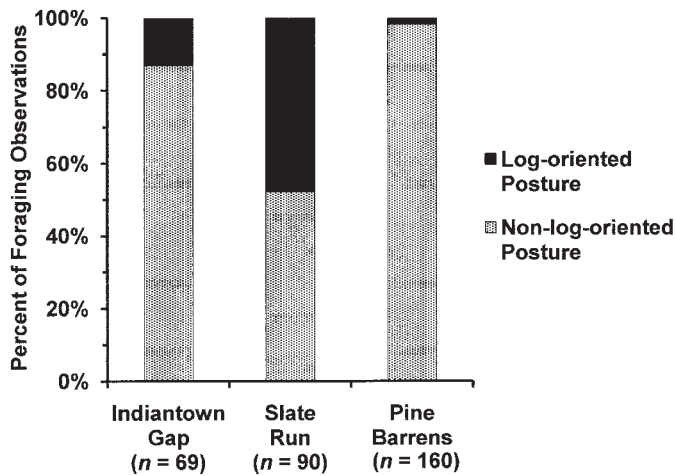


Fig. 5. Observed frequency of log-oriented and non-log-oriented foraging postures of *Crotalus horridus* in different populations. Hawk Mountain is not included because the frequency of the non-log-oriented posture was not recorded for this population. Sample sizes (n) represent the number of observations of foraging, radiotracked animals.

et al., 2005). Such bias could contribute to the lack of continuity between trapping samples and diet samples. However, Anthony et al. (2005) reported that estimates of species diversity (relative abundance) were not altered despite differences in the efficacy of traps to capture different species. Similarly, Woodman et al. (1996) found snap traps to be more effective than Sherman live traps in capturing neotropical small mammals, but found no difference in the relative abundances of small mammals captured by the two trap types. For the small mammals important in our study, Sheppe (1966) found no evidence of trap avoidance in *P. leucopus*, while Chitty and Kempson (1949) reported no evidence of trap avoidance by species of *Microtus*, *Myodes*, or *Sorex* following the first night of trap placement.

Our heavy reliance on medium-sized Sherman live traps could have resulted in an underestimate of the availability of large prey (e.g., *S. carolinensis* and *T. hudsonicus*) and small prey (e.g., *S. cinereus*). However, the dominant prey items in the diet of snakes in all four populations were medium-sized small mammals (*Peromyscus* spp., arvicoline rodents, and *T. striatus*) that are typically sampled effectively with the traps and trapping methods used in our study (J. Merritt, pers. comm.). Our trapping methods were similar to those that have been used in studies designed specifically to estimate the relative abundance of small mammal species (Merritt et al., 2001), and our finding that *Peromyscus* spp. generally occurred in higher relative frequencies than arvicoline rodents at all four locations is consistent with those of similar investigations in forests of the northeastern United States (Yahner, 1992; Elias et al., 2006).

Another factor that could influence estimates of prey availability is the fact that the density of some potential prey species may vary considerably on a microgeographic scale. *Myodes gapperi* seems to be especially distinctive among these mammals in that areas of high population density do not remain constant but shift throughout the landscape in what appear to be cycles of extinction and recolonization (Bowman et al., 2001; Merritt et al., 2001). For example, at Slate Run *M. gapperi* was present in relatively high density in trapping samples in 2003, but nearly absent from the same

trapping grids in 2004–2006 (S. Pelesky, unpubl. data). Because small mammal trapping grids remained stationary during this four-year period, it is possible that *M. gapperi* migrated elsewhere within the study area causing their overall representation in the trapped sample to decline. It is likely that *C. horridus* would be capable of tracking such short-distance population migrations exhibited by *M. gapperi*. This would have allowed the snakes to continue to prey upon *M. gapperi* in relatively high frequency, even when this species was not trapped in any great abundance due to stationary trap placement. As a result, the actual encounter rate with *M. gapperi* may have remained fairly constant for foraging rattlesnakes. However, such “tracking” of a shifting prey population would clearly reflect prey selectivity and constitute an active form of prey preference.

It is likely that temporal variation in the abundance of small mammals on our study sites contributed to observed differences in the foraging behavior and diet of *C. horridus*. Our data collection spanned a period of nearly three decades, observations at each site were combined over multiple years, and not all sampling periods overlapped among the four locations. Most temperate small mammal species, including *P. leucopus*, *P. maniculatus*, *B. brevicauda*, *M. gapperi*, and *T. striatus*, exhibit both seasonal and annual population fluctuations (Wolff, 1996; Merritt et al., 2001; Elias et al., 2006). Based upon behavioral categories similar to those used in the current study, *C. horridus* in Arkansas demonstrated annual variation in the amount of time devoted to foraging (Beaupre, 2008). Decreased foraging activity corresponded to an observed increase in foraging success, which was probably the result of an increase in prey abundance (Beaupre, 2008).

Alternative ambush strategies of *C. horridus* apparently afforded the opportunity to capture a broad diversity of forest prey species. The log-oriented posture (Reinert et al., 1984) was used effectively to capture *Peromyscus* spp. and various squirrel species (especially *Tamias striatus*) that commonly use the upper surface of logs as runways (Sheppe, 1966; Douglass and Reinert, 1982; Barnum et al., 1992). The non-log-oriented foraging position allowed snakes to encounter voles and shrews that travel along established forest floor runways through surface leaf litter and vegetation (Beer, 1961; Hayes and Cross, 1987; Getz et al., 1992). *Peromyscus leucopus* comprised the largest component of the diet at Hawk Mountain, where the log-oriented foraging posture occurred in the highest frequency. In contrast, Pine Barrens snakes exhibited the highest frequency of the non-log-oriented posture, and, concomitantly, the highest proportional consumption of voles and shrews.

In hardwood-dominated forests a large fallen oak tree (*Quercus* spp.) may persist on the forest floor for decades (Mattson et al., 1987), allowing logs and other woody debris to become prominent, structurally stable features in these habitats. Consequently, an individual log may be used consistently as a runway by small mammals and a foraging site for snakes over many years. In contrast to hardwood-dominated sites, the proportion of CWD and size of fallen logs were less at the Pine Barrens site (Reinert, 1984; Reinert and Zappalorti, 1988). The smaller size of logs, higher rates of decomposition of *P. rigida* compared to oaks (Mattson et al., 1987), and frequent wildfires (Little, 1979) contribute to the sparse and comparatively short-term presence of CWD in the Pine Barrens habitat. Despite these differences, the locations selected by foraging snakes in the Pine Barrens

were found to be structurally similar to the sites selected by foraging snakes at the other study sites with respect to the presence of CWD (Reinert, 1993). A multivariate analysis of 12 structural habitat variables also found the percentage of fallen logs to be one of the most influential variables in distinguishing the foraging habitat of *C. horridus* from non-foraging habitat in the Pine Barrens (MacGregor, 1999). Consequently, even where the non-log-oriented posture is the primary foraging strategy (e.g., Pine Barrens), the general presence of logs and other woody debris likely contributes positively to the quality of foraging sites. The frequency of CWD correlates positively with the density of a large variety of small mammals, including species that do not use the upper log surface as runways (Harmon et al., 1986; Hayes and Cross, 1987).

Once an ambush site is selected by *C. horridus*, it may be occupied for a period of several hours to more than two days (Reinert et al., 1984; MacGregor, 1999; Clark, 2006). We found this to be true for both the log-oriented and non-log-oriented postures observed in this study. Forest-floor locations that were occupied for long periods of time or revisited were probably used by multiple prey (or species) and thus represented high quality foraging sites (Charnov, 1976; Clark, 2006). This suggests that, like logs, selected forest-floor sites function as foraging patches where the period of patch occupation is possibly related to a trade-off between patch quality and patch availability (MacArthur and Pianka, 1966).

Klauber (1972:fig. 7:1) illustrated a *Crotalus viridis helleri* (*C. oreganus helleri*) in a “resting coil” nearly identical to the foraging posture described for *C. horridus* (having seven directional changes in the anterior portion of the body). Klauber (1972) suggested that when in such postures a rattlesnake is “resting” and “probably asleep,” and that a rattlesnake in such a “resting position” will often be “settled down” in vegetation or positioned “with one edge of its body against a rock.” This is, in fact, an accurate description of a foraging *C. horridus* and probably applies to other rattlesnake species as well. Likewise, Klauber’s illustration of *Crotalus cerastes* “bedded down in the sand” (Klauber, 1972:fig. 7:4) showed a snake in a posture with a composition nearly identical to that of a foraging *C. horridus*. Klauber contrasted this “resting” posture with a “true striking coil” and suggested that a snake in a resting coil cannot strike an appreciable distance and is reluctant to do so. However, Kardong and Bels (1998:fig. 1) illustrated a pre-strike posture of *C. viridis oreganus* (*C. o. oreganus*) under laboratory conditions that was also similar to that illustrated here for *C. horridus* in the field. Their detailed analysis indicated that rattlesnakes could produce an effective predatory strike from such a posture following a “gate model” of body extension (Kardong and Bels, 1998). Moreover, the close proximity of ambush positions to runways and trails suggests that most predatory strikes by *C. horridus* occur over short distances (Cundall and Beupre, 2001; Cundall, 2002). Our field observations of several prey capture events confirm that *C. horridus* can strike successfully from this foraging posture even at rapidly moving prey. The non-foraging postures that we describe for pre-molt and gravid snakes are perhaps true “resting” postures assumed by snakes for which prey capture is not a primary concern. Such postures appear to afford very limited striking capability.

It appears that there is some plasticity in the use of differing foraging postures among snakes within a population. Several

individual snakes were observed to use both log-oriented and non-log-oriented foraging postures when observed on different occasions. Although no experimental analysis was performed to assess the ability of snakes to alter their foraging response to prey behavior and availability, some interesting insights can be gained from observations of translocated *C. horridus*. Reinert and Rupert (1999) introduced 11 individuals of *C. horridus* into the Hawk Mountain study site from three geographically disjunct sites in Pennsylvania (four snakes were from the vicinity of the Indiantown Gap population, two were from a population adjacent to Slate Run, and five were from the Pocono Plateau region of northeastern Pennsylvania). The current study indicates that the Indiantown Gap population differed in the frequency of both its prey consumption and foraging posture from those of the Hawk Mountain Sanctuary population, and it is likely that the other populations also exhibited similar geographic variation with regard to their foraging ecology. However, following translocation to Hawk Mountain, this sample of snakes exhibited a frequency of log-oriented foraging behavior that did not differ from that of resident snakes during the same time period (Reinert and Rupert, 1999). Consequently, foraging posture may be based upon a direct assessment of the quality of different options (patch quality) in the environment. If the top surface of a log is heavily scented by mice and/or chipmunks, a log-oriented foraging posture would optimize contact with a potential prey. On the other hand, if a site had a high density of voles and runways exist through the litter or along the sides of logs and rocks, the non-log-oriented foraging posture in the leaf litter that provided surveillance of the runway would have a greater potential for success. We envision that an experimental approach similar to that of Clark (2004) could be devised to assess the extent of this type of plasticity within individuals.

This study demonstrates that geographic variation in the diet of *C. horridus* is reflected by similar variation and potential individual plasticity in foraging behavior. Variability in the composition of prey populations and past experience may strongly influence rattlesnake predatory behavior (Clark, 2004, 2007). The considerable variation in diet among populations of *C. horridus* indicates that large-scale, species-wide examinations may not always be representative of the diet of local populations. Likewise, simple estimates of prey availability may not be predictive of the level of prey consumption for some ambush predators.

Effective predators evolve foraging behaviors that increase their prey encounter rates. This study shows *C. horridus* to be a generalist predator upon a broad diversity of prey species whose populations may be both spatially and temporally dynamic. Our findings also suggest that *C. horridus* has the behavioral flexibility to alter its ambush posture to selectively foraging for those prey that can be encountered most effectively in a given habitat.

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