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Diet of the Timber Rattlesnake, *Crotalus horridus*

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The diet of a species is one of the defining aspects of its ecology, and detailed information on food habits is often necessary to approach broader ecological or behavioral questions. This is particularly true for snakes: detailed dietary information has been the basis for studies of foraging behavior (Lind and Welsh, 1994), predator-prey coevolution (Brodie and Brodie, 1990; Downes and Shine, 1998; Heatwole and Powell, 1998), behavioral genetics (Arnold, 1980; Burghardt, 1993), optimal foraging theory (Arnold, 1993), community ecology (Cadle and Greene, 1993), and the evolutionary origins of specialized morphologies (Greene, 1983; Pough and Groves, 1983). However, despite its importance, detailed knowledge of food habits is often lacking, even in well-studied species, such as the timber rattlesnake, *Crotalus horridus*.

The timber rattlesnake is a widespread viperid in the deciduous forests of the eastern third of the United States. It is the model organism for numerous research programs (summarized in Brown, 1993), yet some basic aspects of its ecology, including its natural diet, are still relatively poorly known. Even though several accounts have been published (summarized in Table 1), they consist mainly of lists of prey taken by individual snakes from a localized area. Almost nothing is known about how diet varies ontogenetically, seasonally, or geographically.

I examined the feeding ecology of *C. horridus* by synthesizing previously published dietary records with new information about the stomach contents of museum specimens. Geographic variation in diet was assessed by comparing the food habits of snakes from the northern deciduous forest province with snakes from the southern coastal plain and mixed forest province. I also analyzed ontogenetic dietary variation by comparing the size of snakes that specialize on

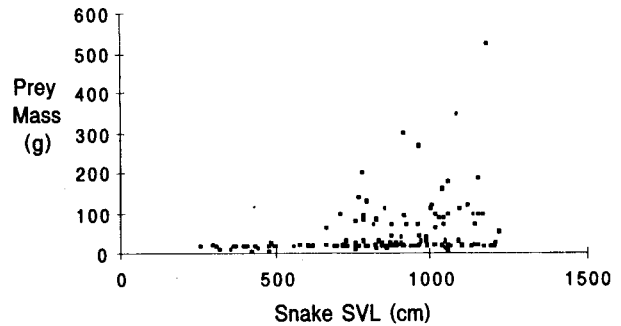


FIG. 1. Relationship between prey mass and snake body size (SVL) in *Crotalus horridus* ($N = 144$). The shape of the plot shows that larger snakes expand their diet to include larger prey items but do not eliminate small items from their diet as they grow.

specific prey taxa. The resulting dietary database not only fills a gap in our knowledge of the natural history of this species but may also serve as a foundation for further research on predator-prey interactions, foraging behavior, habitat use, and community structure.

I examined all available preserved specimens of *C. horridus* ($N = 1108$) in the collections of Cornell University, Carnegie Museum of Natural History, University of Michigan Museum of Zoology, Chicago Academy of Sciences, Field Museum of Natural History, University of Illinois Museum of Natural History, Illinois Natural History Survey, New York State Museum, National Museum of Natural History, North Carolina State Museum, University of Florida, Auburn University Museum, and University of Kansas Natural History Museum. I checked each specimen for stomach contents by making a midventral incision, omitting only fragile individuals and those specimens whose collection information indicated that they were not likely to contain stomach contents (i.e., there was a significant discrepancy between the date of collection and the date of preservation). For each snake with prey in its stomach, I recorded collection locality, snout-vent length ($SVL \pm 1$ cm), sex, body mass without stomach contents (± 1 g) and the number of items in the stomach. When possible, I also recorded direction of ingestion. All snakes were weighed after being blotted dry with paper towels. Stomach contents were identified to as low a taxonomic level as possible by comparison with museum specimens, or from microscopic examination of hair (Adorjan and Kolenosky, 1969). The mass at time of ingestion was estimated for relatively intact prey items by comparing them to conspecific specimens deposited in the Cornell University museum. This was not possible for several items, which consisted of only fur or feathers. Specimens that I suspected were fed in captivity were excluded from analysis.

When possible, I have incorporated previously published dietary records of *C. horridus* (listed in Table 1) in the analyses presented in this paper. However, most previously published dietary records contain only information on general locale and prey identity and so are of limited use.

For analysis of geographic variation in diet, I used a map of potential natural vegetation (Kuchler, 1985) to divide the specimens into two groups—one from

the laurential mixed and eastern deciduous forest provinces, and the other from the southeastern mixed, coastal plain, and prairie parkland forest provinces. This translates broadly into a north-south division.

Statistical analyses were performed using the software program Minitab. Values given are mean \pm 1 SD, all *P*-values are two-tailed, and $\infty \leq 0.05$ was the significance level for all tests.

Of the 1108 specimens examined, 178 (16.1%) contained prey items in their stomachs. A total of 189 prey items were identified from these snakes (SVL = 80.5 ± 23.8 cm, range = 25.1–121.2 cm; mass = 526.6 ± 384.6 , range = 23–1509 g). With the addition of 400 literature records of prey, 537 (91.1%) of 589 items were mammals, 42 (7.2%) were birds, seven (1.2%) were reptiles, and two (0.3%) were amphibians. Important mammalian genera in the diet of *C. horridus* (those that form more than 1% of the total number of prey records) include *Peromyscus* (33.3%), *Microtus* (10.9%), *Tamias* (10.6%), *Sylvilagus* (10.4%), *Sigmodon* (5.3%), *Sciurus* (4.2%), *Clethrionomys* (3.4%), *Napaeozapus* (2.6%), *Sorex* (2.2%), *Mus* (2.2%), and *Blarina* (1.2%). Eleven other mammalian genera make up an additional 5.2% of the prey records (Table 1).

Of the 134 items for which direction of ingestion could be determined, 133 were swallowed head first. The sole exception was a relatively small item, a smoky shrew (*Sorex fumeus*) eaten by a female 74 cm in SVL.

The minimum number of prey contained in each stomach could be determined for 167 of the specimens. Of these, 145 (87.3%) contained a single item, 19 (10.9%) contained two items, and three (1.8%) contained three items. Individuals with multiple prey items (SVL = 90.8 ± 19.1 cm, *N* = 22) were significantly larger than those containing a single item (SVL = 78.1 ± 28.6 cm, *N* = 145; ANOVA, *F* = 4.86, *P* = 0.03). Of those individuals with more than one prey item, 12 (54.5%) contained more than one species of prey, whereas 10 (45.5%) contained more than one individual of the same species.

The range of *C. horridus* was divided geographically into two groups, as described in the methods section. The line dividing these groups runs roughly from the border of North Carolina and Virginia, across the tops of Georgia, Alabama and Mississippi, and through the middle of Arkansas to the border of Oklahoma and Texas. The diet of *C. horridus* from these two regions differed significantly (Table 2). Specimens from the northern portion of the range preyed on a greater number of *Microtus* (64 of 455 in north, zero of 134 in south), *Tamias* (61 of 455 in north, one of 134 in south), *Napaeozapus* (15 of 455 in north, zero of 134 in south), and *Clethrionomys* (20 of 455 in north, zero of 134 in south). Specimens from the southern region preyed on a greater number of *Sigmodon* (one of 455 in north), *Sylvilagus* (39 of 455 in north, 22 of 134 in south), *Ochrotomys* (zero of 455 in north, four of 134 in south), and *Mus* (four of 455 in north, nine of 134 in south). There were no geographic differences in the frequency of predation on the remaining prey taxa.

Additionally, the diet of *C. horridus* shows considerable ontogenetic variation (Table 3). I was able to obtain information on snake size for 204 of the prey records in this study. Sixty-six of these 204 records were from juvenile or subadult snakes (snakes less

than 75 cm in SVL), whereas 138 of them were from adults (snakes 75 cm or greater in SVL). Subadults preyed on a greater number of *Sorex* (seven of 66 for subadults, one of 138 for adults), *Blarina* (three of 66 for subadults, zero of 138 for adults), *Ochrotomys* (four of 66 for subadults, zero of 138 for adults), and *Peromyscus* (40 of 66 for subadults, 46 of 138 for adults). Adults preyed on a greater number of *Microtus* (one of 66 for subadults, 16 of 138 for adults), *Sigmodon* (two of 66 for subadults, 20 of 138 for adults), *Tamias* (one of 66 for subadults, 14 of 138 for adults), and *Sylvilagus* (zero of 66 for subadults, 10 of 138 for adults). All of the taxa consumed more frequently by subadults are relatively small (25 g or less), whereas those consumed more frequently by adults are larger (35 g or more).

I obtained reliable mass estimates for 144 prey items. As can be seen from Figure 1, larger snakes expand their diet to include larger prey species. However, large timber rattlesnakes did not eliminate smaller prey items from their diet, as do some other snake species (Arnold, 1993).

Among mammalian prey taken by *C. horridus*, the most commonly eaten species were abundant small woodland mammals (Whitaker and Hamilton, 1998). This suggests that *C. horridus* consume prey in proportion to their availability in the area in which they forage. Indeed, Reinert et al. (1984) found that *C. horridus* in north central Pennsylvania consumed small mammals in proportion to their occurrence at his study site. Therefore, dietary variation between northern and southern parts of the range of *C. horridus* (Table 2) is probably a result of differing availability of various species of small mammals. However, it is possible that over evolutionary time, different timber rattlesnake populations have undergone adaptation to specialize on finding and consuming the most abundant small mammals in their areas. If true, then the geographic dietary variation found in this species is an important factor to consider when comparing behavioral, ecological, or physiological traits of *C. horridus* from different populations.

The idea that *C. horridus* opportunistically feeds on whatever small mammals are available is supported by the fact that there is a certain amount of intraindividual dietary variation. Over half of those individuals that contained multiple prey items in their stomach had preyed upon more than one species, indicating that individuals probably do not specialize on only a few of the available prey species.

In addition to geographic variation, *C. horridus* exhibits significant ontogenetic dietary variation, as do most snake species (Mushinsky, 1987; Arnold, 1993). Small timber rattlesnakes prey mostly on very small mammals, such as shrews (*Sorex* spp.), white-footed mice (*Peromyscus*) and house mice (*Mus musculus*). In contrast to snake species that eliminate smaller items from their diet as they grow (Arnold, 1993), timber rattlesnakes continue to consume these species as adults. However, as they grow, their diet does expand to include larger items, such as chipmunks (*Tamias striatus*), cotton rats (*Sigmodon hispidus*), squirrels (*Sciurus* spp.), and rabbits (*Sylvilagus* spp.). The result is a significant difference in the importance of particular prey types in the diets of adult and juvenile snakes (Table 3).

TABLE 1. Prey eaten by *Crotalus horridus*. "Frequency" refers to the number of times each prey taxon was found in the entire sample, including stomach contents identified from museum specimens in this study and all available literature records of prey.

Prey taken	Frequency	% of total	Source
AMPHIBIA			
Unidentified anuran	2	0.34	Uhler et al., 1939
REPTILIA			
Squamata			
Scincidae			
<i>Eumeces laticeps</i>	1	0.17	Hamilton and Pollack, 1955
<i>Scincella lateralis</i>	2	0.34	Hamilton and Pollack, 1955
Teiidae			
<i>Cnemidophorus</i> sp.	3	0.51	Hamilton and Pollack, 1955
Serpentes			
Colubridae			
<i>Coluber constrictor</i>	1	0.17	Fitch, 1982
AVES			
Coraciiformes			
Picidae			
<i>Melanerpes carolinus</i>	1	0.17	Hamilton and Pollack, 1955
Galliformes			
Phasianidae			
<i>Bonasa umbellus</i>	1	0.17	Uhler et al., 1939
<i>Colinus virginianus</i>	6	1.02	Uhler et al., 1939; Clark, 1949
Passeriformes			
<i>Melospiza melodia</i>	1	0.17	This study
<i>Passer domesticus</i>	2	0.17	This study
Unidentified passeriform	21	3.58	Anderson, 1965; Palmer and Braswell, 1995; Uhler et al., 1939
Unidentified bird sp.	10	1.71	Bush, 1959; Hamilton and Pollack, 1955; Savage, 1967; Reinert et al., 1984; this study
MAMMALIA			
Carnivora			
Mustelidae			
<i>Mustela vison</i>	2	0.34	Savage, 1967; Klauber, 1956
Chiroptera			
Vespertilionidae			
<i>Eptesicus fuscus</i>	1	0.17	Anderson, 1965
<i>Myotis</i> sp.	1	0.17	Keenlyne, 1967
Unidentified bat sp.	1	0.17	Uhler et al., 1939
Insectivora			
Soricidae			
<i>Blarina brevicauda</i>	6	1.02	Babcock, 1929; Uhler et al., 1939; this study
<i>Blarina</i> sp.	1	0.17	Palmer and Braswell, 1995
<i>Cryptotis parva</i>	4	0.68	Fitch, 1982; Uhler et al., 1939
<i>Sorex cinereus</i>	1	0.17	Smyth, 1949
<i>Sorex fumeus</i>	2	0.34	This study
<i>Sorex longirostris</i>	3	0.51	This study
<i>Sorex</i> sp.	7	1.19	Surface, 1906; Uhler et al., 1939; this study
Lagomorpha			
Leporidae			
<i>Sylvilagus aquaticus</i>	1	0.17	Dundee and Rossman, 1989
<i>Sylvilagus floridanus</i>	43	7.34	Fitch, 1982; Klauber, 1956; Reinert et al., 1984; Uhler et al., 1939; this study
<i>Sylvilagus</i> sp.	18	3.07	Clark, 1949; Hamilton and Pollack, 1955; Palmer and Braswell, 1995; Surface, 1906; this study
Rodentia			
Dipodidae			
<i>Napaeozapus insignis</i>	13	2.22	Barbour, 1950; Savage, 1906; Smyth, 1949; Uhler et al., 1939; this study
<i>Zapus hudsonicus</i>	2	0.34	Fitch, 1982; Surface, 1906
Muridae			
<i>Clethrionomys gapperi</i>	20	3.41	Barbour, 1950; Reinert et al., 1984, Savage, 1967; Smyth, 1949; Uhler et al., 1939; this study

TABLE 1. Continued.

Prey taken	Frequency	% of total	Source
<i>Microtus chrotorrhinus</i>	8	1.37	Savage, 1967
<i>Microtus ochrogaster</i>	5	0.85	Fitch, 1982; this study
<i>Microtus pennsylvanicus</i>	28	4.78	Babcock, 1929; Keenlyne, 1972; Surface, 1906; this study
<i>Microtus pinetorum</i>	7	1.19	Fitch, 1982; Uhler et al., 1939; this study
<i>Microtus</i> sp.	16	2.73	Uhler et al., 1939; this study
<i>Mus musculus</i>	13	2.22	Fitch, 1982; Palmer and Braswell, 1995; this study
<i>Neotoma floridiana</i>	3	0.51	Fitch, 1982
<i>Neotoma magister</i>	1	0.17	Smyth, 1949
<i>Ochrotomys nuttali</i>	4	0.68	This study
<i>Oryzomys palustris</i>	1	0.17	Palmer and Braswell, 1995
<i>Peromyscus gossypinus</i>	2	0.34	This study
<i>Peromyscus leucopus</i>	56	9.56	Bush, 1959; Fitch, 1982; Klauber, 1956; Smyth, 1949; Surface, 1906; this study
<i>Peromyscus maniculatus</i>	15	2.56	Barbour, 1950; Smyth, 1949; this study
<i>Peromyscus</i> sp.	122	20.82	Hamilton and Pollack, 1955; Keenlyne, 1972; Reinert et al., 1984; Savage, 1967; Smyth, 1949; Uhler et al., 1939; this study
<i>Rattus rattus</i>	2	0.34	Surface, 1906; this study
<i>Sigmodon hispidus</i>	32	5.46	Anderson, 1965; Fitch, 1982; Hamilton and Pollack, 1955; Palmer and Braswell, 1995; this study
<i>Synaptomys cooperi</i>	1	0.17	Smyth, 1949
Sciuridae			
<i>Glacomys volans</i>	4	0.68	Savage, 1967; Uhler et al., 1939
<i>Sciurus carolinensis</i>	17	2.56	Bush, 1959; Fitch, 1982; Hibbard, 1936; King, 1939; Keenlyne, 1972; Palmer and Braswell, 1995; Uhler et al., 1939; this study
<i>Sciurus niger</i>	1	0.17	Fitch, 1982
<i>Sciurus</i> sp.	7	1.19	Anderson, 1965; Clark, 1949; Savage, 1967
<i>Tamias striatus</i>	62	10.58	Barbour, 1950; Keenlyne, 1972; Reinert et al., 1984; Savage, 1967; Smyth, 1949; Uhler et al., 1939; this study
<i>Tamiasciurus hudsonicus</i>	5	0.85	King, 1939; Surface, 1906; this study

The behavioral basis for this ontogenetic shift could simply be a reflection of the ability of larger snakes to consume larger prey. However, water snakes (*Nerodia erythrogaster*) undergo an ontogenetic shift in diet that is proximally caused by an intrinsic shift in the pref-

erence for prey-derived chemical cues (Mushinsky and Lotz, 1980). Like many viperids that use a sit-and-wait foraging strategy, timber rattlesnakes use chemical cues left by potential prey items to select ambush sites (Reinert et al., 1984; Duvall et al., 1990). Therefore,

TABLE 2. Percent occurrence of different mammalian prey species in the diet of *Crotalus horridus* from Northern ($N = 456$) and southern ($N = 134$) regions. A map of potential natural vegetation (Kuchler, 1985) was used to divide snakes into a northern group that occurs in laurential mixed and eastern deciduous forests and a southern group that occurs in southeastern mixed, coastal plain, and prairie parkland forests. Nonsignificant results denoted by "ns." * significance based on chi-square test. ** significance based on Fisher's exact test.

Prey species	Northern region	Southern region	P-value
New World mice (all <i>Peromyscus</i> spp.)	34.9	27.6	ns
Voles (all <i>Microtus</i> spp.)	14.1	0.0	<0.0001*
Eastern chipmunk (<i>Tamias striatus</i>)	13.5	0.7	<0.0001*
Cottontail rabbits (all <i>Sylvilagus</i> spp.)	8.6	16.4	0.009*
Cotton rat (<i>Sigmodon hispidus</i>)	0.2	22.4	<0.0001*
Squirrels (all <i>Sciurus</i> spp.)	3.3	5.2	ns
Red-backed vole (<i>Clethrionomys gapperi</i>)	4.4	0.0	0.01**
Jumping mouse (<i>Napaeozapus insignis</i>)	3.3	0.0	0.02**
Golden mouse (<i>Ochrotomys nuttali</i>)	0.0	3.0	0.002**
Shrews (all <i>Sorex</i> spp.)	2.0	3.0	ns
House mouse (<i>Mus musculus</i>)	0.9	6.7	0.0004**
Short-tailed shrews (all <i>Blarina</i> spp.)	0.0	3.0	0.003**

TABLE 3. Percent occurrence of different mammalian prey species in the diet of juvenile (SVL < 75 cm, N = 66) and adult (SVL > 75 cm, N = 138) *Crotalus horridus*. Prey species listed in order of approximate size, from smallest to largest (Whitaker and Hamilton, 1998). Juvenile snakes prey mainly on items that are 25 g or less, whereas the majority of the adult diet consists of items that are 35 g or more. Nonsignificance denoted by "ns." * significance based on chi-square test. ** significance based on Fisher's exact test.

Prey species	Approximate mass (g)	Juveniles	Adults	P-value
Shrews (all <i>Sorex</i> spp.)	8	10.6	0.7	0.002**
Short-tailed shrew (<i>Blarina brevicauda</i>)	13	4.5	0.0	0.03**
House mouse (<i>Mus musculus</i>)	19	7.6	2.9	ns
Golden mouse (<i>Ochrotomys nuttali</i>)	22	6.1	0.0	0.01**
New World mice (all <i>Peromyscus</i> spp.)	25	60.6	33.3	0.0005*
Red-backed vole (<i>Clethrionomys gapperi</i>)	25	1.5	3.6	ns
Voles (all <i>Microtus</i> spp.)	35	1.5	11.6	0.01**
Cotton rat (<i>Sigmodon hispidus</i>)	100	3.0	14.5	0.01**
Eastern chipmunk (<i>Tamias striatus</i>)	110	1.5	10.1	0.02**
Grey squirrel (<i>Sciurus carolinensis</i>)	200–500	1.5	5.8	ns
Cottontail rabbit (<i>Sylvilagus floridiana</i>)	500–1000	0.0	7.3	0.03**

perhaps the ontogenetic dietary variation exhibited by snake species that employ this ambush tactic is also mediated by an intrinsic shift in the preference for prey-derived chemical cues.

In comparison with other crotalines (Klauber, 1956; Mushinsky, 1987; Greene, 1992), timber rattlesnakes exhibit an unusual degree of specialization on endotherms, even as juveniles. Unfortunately, none of the literature records for timber rattlesnakes eating ectothermic prey include data on snake size, making it impossible to evaluate any possible ontogenetic shift from ectotherms to endotherms. Among those 201 prey records for which data on snake size were available, none contained ectothermic prey; even the neonates with prey in their stomach contained small mammals. This is surprising, given that ectothermic prey (lizards, frogs, other snakes, invertebrates, etc.) are abundant in habitats where timber rattlesnakes live, and readily taken by sympatric crotaline snakes, such as *Agkistrodon* (Uhler et al., 1939; Hamilton and Pollack, 1955; Savage, 1967; Fitch, 1982) and *Sistrurus* (Hamilton and Pollack, 1955; Keenlyne and Beer, 1973). Among other rattlesnake species, most exhibit an ontogenetic dietary shift from ectotherms to endotherms (Klauber, 1956); evidence of feeding almost exclusively on endotherms exists for only a few species. These include *C. durissus* (Salamao et al., 1995) and *C. molossus* (H. W. Greene, pers. comm.). Klauber (1956) groups *C. molossus*, *C. durissus*, *C. horridus* and *C. basiliscus* together in the "durissus group," which indicates that extreme specialization on endotherms is most likely an ancestral trait for this group. There may be several reasons why members of the *durissus* group do not prey on ectotherms as juveniles, as other rattlesnake species do. Behavioral and physiological changes necessary to switch from finding and consuming relatively sedentary ectotherms to finding and consuming fast, active endotherms might be costly. Additionally, the microhabitat to which these species are adapted may not be used by local populations of amphibians and reptiles that could serve as appropriate prey (Reinert, 1984).

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