

ARTICLES

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Food Habits of Sympatric Pitvipers from the West Gulf Coastal Plain, USA

Widespread species that occupy multiple communities exhibit geographic variation in their natural history due to the ecological context of the local community. An animal's food habitats are a central component to understanding its natural history and ecological role within its community—information that is critical to understanding resource needs of a species, mechanisms of species coexistence, and energy flow in food webs (Litvaitis 2000; Schalk et al. 2014). This information is also crucial for predicting the response of populations to changes in resource availability and, if necessary, inform mitigation strategies (Holycross and Mackessy 2002).

The West Gulf Coastal Plain (WGCP) ecoregion is delineated as occurring west of the Mississippi Embayment and south of the Interior Highlands (MacRoberts and MacRoberts 2003). It is a region of poorly consolidated sediments of Miocene to Pleistocene age with low topographic relief extending inland from the Gulf of Mexico (Bernard and Leblanc 1965). The ecoregion includes significant portions of western Louisiana and eastern Texas, portions of southern Arkansas, and a limited portion of southeastern Oklahoma. Historically, the region was greatly influenced by a fire regime consisting of frequent, low intensity fires resulting in the widespread dominance of Longleaf Pine (*Pinus palustris*) and other pine species in the uplands (Bridges and Orzell 1989; Frost 2006). More mesic forests dominated by hardwood species tended to dominate in lower topographic areas (primarily along drainages) with a less intense fire regime.

Four species of pitvipers occur in sympatry on the WGCP: Eastern Copperhead (*Agkistrodon contortrix*), Northern Cottonmouth (*A. piscivorus*), Timber Rattlesnake (*Crotalus horridus*), and Pygmy Rattlesnake (*Sistrurus miliarius*). These species are broadly distributed across much of the southern/central/eastern United States and utilize multiple habitat types

across their range (Ernst and Ernst 2011). Their diet has been examined and synthesized across much of their range, yet there is little information on their feeding habitats from the WGCP. To contribute to the understanding of the geographic variation in natural history of these widespread pitvipers, we collected additional information on the feeding habitats of these four species in the WGCP through opportunistic fecal and stomach content analysis.

METHODS

Fecal samples were collected from snakes that were captured using four-entrance funnel traps (see Burgdorf et al. 2005 for trap design), in Anderson, Angelina, Jasper, Nacogdoches, Newton, Sabine, and Wood counties in eastern Texas and Natchitoches, Vernon, and Winn parishes in west-central Louisiana (Fig. 1). The general habitat is mesic forest dominated by pines in the uplands and mixed hardwood and pine-hardwood forests on lower slopes and bottomlands. Individuals of *A. contortrix*, *A. piscivorus*, and *S. miliarius* were predominately captured in upland pine habitats, often from sites characterized by sandy, well-drained soils. Most *C. horridus* were captured in hardwood-dominated forests on or

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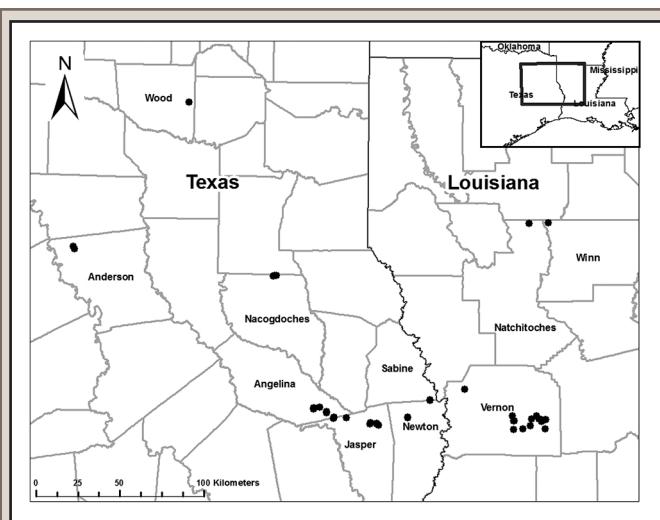


FIG. 1. Location of snake traps and snake road-kill collection points (both represented by black dots) in Anderson, Angelina, Jasper, Nacogdoches, Newton, Sabine, and Wood counties in eastern Texas and Natchitoches, Vernon, and Winn parishes in west-central Louisiana.

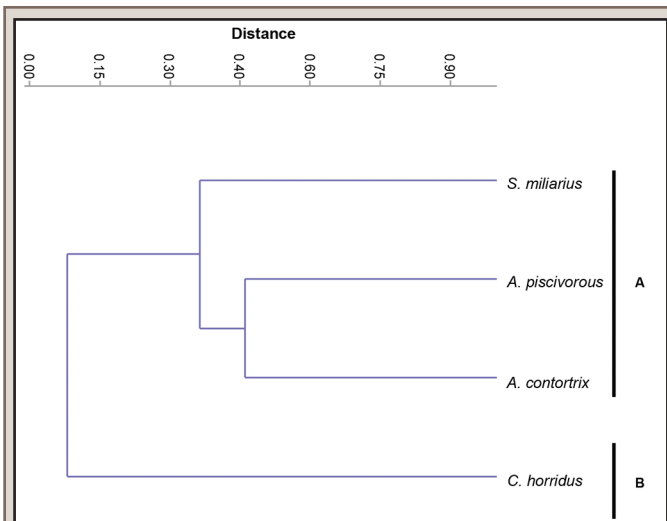


FIG. 2. UPGMA phenogram showing relationships between the four viper species based on prey items (Jaccard similarity index; cophenetic correlation = 0.9807). Species that share the same letter are not significantly different from one another (PERMANOVA; P [perm] = 0.0002).

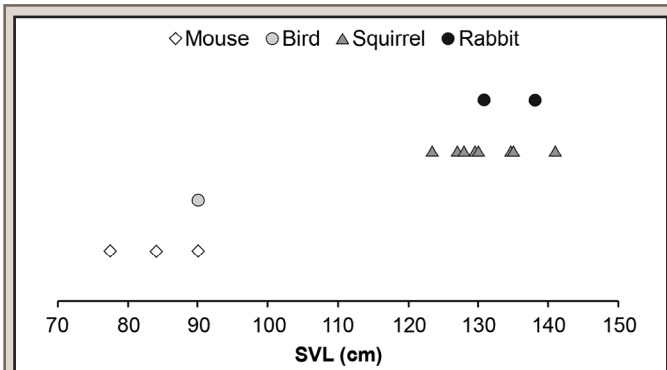


FIG. 3. Association between prey class and snake snout-vent length for *Crotalus horridus* from the West Gulf Coastal Plain of Texas and Louisiana (N = 20). Presence of prey was determined via fecal and stomach contents analysis.

adjacent to the floodplains of rivers and major streams. Snakes were held in the laboratory for sufficient time to pass prey items (typically a week), followed by release at point of capture. Fecal samples were stored in 80% ethanol prior to examination. We also examined the stomach contents of road-killed individuals that were opportunistically collected during the course of the study. Road-killed individuals were more generally distributed across different habitats.

Using a dissecting microscope, prey remains (primarily bone, hair, and scales) were visually identified to the lowest taxon feasible through comparison with published illustrations, museum specimens, and hair and bone samples obtained from local species of potential prey. For each prey type, we report the number of individual prey items, the numerical frequency of prey items, and the frequency of occurrence in fecal samples and stomach contents. To examine patterns of similarity of diet among the four snake species, we generated a dendrogram using Unweighted Pair Group Method with Arithmetic mean (UPGMA) cluster method using Jaccard's similarity index. We also compared the prey composition among the four species using permutational multivariate analysis of variance (PERMANOVA). Finally, we also report the ontogenetic variation

in prey for a subset of *C. horridus* for which we have body size data. All analyses were conducted in the program PAST (ver. 2.16; Hammer et al. 2001).

RESULTS

We examined a total of 138 snake fecal samples from the four snake species (*A. contortrix* [N = 49 fecal samples], *A. piscivorus* [N = 55 fecal samples], *C. horridus* [N = 17 fecal samples], *S. miliarius* [N = 17 fecal samples]) and 14 snake stomachs from road-killed individuals of three species (*A. contortrix* [N = 2], *A. piscivorus* [N = 2], *C. horridus* [N = 10]). From the fecal samples and stomach contents, we identified prey including invertebrates, reptiles, birds, and mammals. There was a significant difference in prey composition of *C. horridus* compared to the other three species of pitvipers (PERMANOVA, $F = 1.99$, P [perm] = 0.0002, Fig. 2). However, the other three species of pitvipers did not exhibit significant differences in prey composition.

Agkistrodon contortrix preyed upon a wide variety of prey including invertebrates, reptiles, birds, and mammals (Tables 1 and 2). *Agkistrodon contortrix* preyed upon nearly 60% of the prey types identified. Invertebrates were documented in over 50% of the fecal samples, followed by mammals (nearly 26%), reptiles (21%), and birds (2%) (Table 1). Mammal prey primarily consisted of small-bodied individuals such as mice and shrews (Table 1). Similarly, *A. piscivorus* preyed upon a wide variety of animals including invertebrates, reptiles, birds, and mammals (Tables 1 and 2) which represented 53% of the prey documented. Invertebrates and reptiles were nearly equal in their frequency of occurrence in the fecal samples (nearly 35% and 30%, respectively), followed by mammals (nearly 21%), and birds (9%) (Table 1).

Unlike the two species of *Agkistrodon*, *C. horridus* had a lower diversity of prey items found in the fecal samples and stomach contents (Tables 1 and 2), representing only 26% of the prey types. Mammals comprised nearly 90% of the identified prey in fecal samples, followed by birds and invertebrates in equal proportion (6%). However, the single invertebrate detected in the *C. horridus* fecal sample was a botfly larva, which was likely secondarily ingested when a rabbit was consumed. No reptile prey were observed in the fecal samples (Table 1). Compared to the mammal prey of the two *Agkistrodon* species, larger-bodied rabbits and squirrels were detected more frequently than smaller rodents in *C. horridus* fecal samples. Examination of ten stomachs from road-killed individuals of *C. horridus* revealed a similar pattern, with prey consisting exclusively of endotherms (90% mammals and 10% birds) (Table 2). In addition to larger-bodied mammal species, examination of stomach contents revealed the presence of small-bodied *Peromyscus* sp. (Table 2). Ontogenetically, *C. horridus* shifted from consuming mice to larger-bodied squirrel and rabbit prey with increasing body size (Fig. 3).

Similar to *C. horridus*, *S. miliarius* had a low diversity of prey items detected in the fecal samples, containing only 32% of the prey types (Table 1). Mammals were the most frequent prey found in the fecal samples of *S. miliarius*, though at a much lower frequency compared to *C. horridus* (47%), followed by reptiles (29%), and then invertebrates (17%) (Table 1). No birds were detected in *S. miliarius* fecal samples. Unlike *C. horridus*, the mammalian prey of *S. miliarius* were primarily small-bodied mice and shrews (Table 1). Skinks (*Plestiodon* spp.) were also detected across nearly one fourth of the fecal samples. No stomach contents of *S. miliarius* were examined.

TABLE 1. The number of individual prey items (n), the numerical frequency of prey (%N), and the frequency of occurrence of prey items across individuals (%FO) found in fecal samples in four species of sympatric pitvipers from the West Gulf Coastal Plain of Texas and Louisiana, USA. N = the number of fecal samples analyzed for each species. Taxa marked with an asterisk (*) were likely incidental consumptions.

Taxon	<i>Agkistrodon contortrix</i> N = 49			<i>Agkistrodon piscivorus</i> N = 55			<i>Crotalus horridus</i> N = 17			<i>Sistrurus miliarius</i> N = 17		
	n	%N	%FO	n	%N	%FO	n	%N	%FO	n	%N	%FO
Invertebrates												
Araneae	4	6.5	8.2	-	-	-	-	-	-	1	5.3	5.9
Coleoptera	1	1.6	2.0	1	1.6	1.8	-	-	-	-	-	-
Oestridae larva*	-	-	-	-	-	-	1	5.3	5.9	-	-	-
Cicadae	-	-	-	1	1.6	1.8	-	-	-	-	-	-
Lepidoptera adult	2	3.2	2.0	-	-	-	-	-	-	-	-	-
<i>Solenopsis invicta</i> *	-	-	-	1	1.6	1.8	-	-	-	-	-	-
Unidentified ant*	1	1.6	2.0	2	3.2	3.6	-	-	-	1	5.3	5.9
Insect eggs*	13	21.0	4.1	2	3.2	1.8	-	-	-	-	-	-
Unidentified insect	11	17.7	20.4	15	23.8	18.2	-	-	-	2	10.5	5.9
Aves												
Unidentified bird	1	1.6	2.0	5	7.9	9.1	1	5.3	5.9	-	-	-
Mammalia												
<i>Sylvilagus floridanus</i>	1	1.6	2.0	-	-	-	1	5.3	5.9	-	-	-
<i>Sylvilagus</i> sp.	-	-	-	-	-	-	2	10.5	11.8	-	-	-
<i>Mus</i> sp.	-	-	-	-	-	-	2	10.5	5.9	-	-	-
<i>Peromyscus</i> sp.	6	9.7	12.2	2	3.2	3.6	-	-	-	1	5.3	5.9
<i>Reithrodontomys fulvescens</i>	1	1.6	2.0	1	1.6	1.8	-	-	-	-	-	-
<i>Sciurus carolinensis</i>	-	-	-	-	-	-	7	36.8	41.2	-	-	-
<i>Sciurus niger</i>	-	-	-	-	-	-	1	5.3	5.9	-	-	-
<i>Sciurus</i> sp.	-	-	-	-	-	-	1	5.3	5.9	-	-	-
<i>Sigmodon hispidus</i>	-	-	-	5	7.9	9.1	-	-	-	-	-	-
<i>Blarina carolinensis</i>	1	1.6	2.0	-	-	-	-	-	-	2	10.5	11.8
<i>Cryptotis parva</i>	-	-	-	-	-	-	-	-	-	1	5.3	5.9
Unidentified shrew	3	4.8	6.1	-	-	-	-	-	-	1	5.3	5.9
Unidentified mammal	4	6.5	8.2	5	7.9	9.1	3	15.8	17.6	3	15.8	17.6
Reptilia												
<i>Anolis carolinensis</i>	2	3.2	4.1	-	-	-	-	-	-	-	-	-
<i>Sceloporus undulatus</i>	-	-	-	2	3.2	3.6	-	-	-	1	5.3	5.9
<i>Plestiodon</i> spp.	2	3.2	4.1	2	3.2	5.5	-	-	-	5	26.3	23.5
<i>Aspidoscelis sexlineata</i>	1	1.6	2.0	3	4.8	3.6	-	-	-	-	-	-
<i>Terrapene carolina</i>	-	-	-	6	9.5	7.3	-	-	-	-	-	-
Reptile eggs	1	1.6	2.0	-	-	-	-	-	-	-	-	-
Unidentified lizard	4	6.5	8.2	1	1.6	1.8	-	-	-	-	-	-
Unidentified snake	2	3.2	4.1	5	7.9	9.1	-	-	-	-	-	-
Unidentified reptile	1	1.6	2.0	-	-	-	-	-	-	-	-	-
Unknown Vertebrate												
Unidentified vertebrate	-	-	-	4	6.3	7.3	-	-	-	1	5.3	5.9

DISCUSSION

The broad diet of *Agkistrodon contortrix* is well documented, with prey ranging from invertebrates to ectothermic vertebrates (frogs and lizards) to endothermic vertebrates (mammals and birds) (Ernst and Ernst 2011). However, dietary composition varies across populations and appears to be linked to prey availability across different habitats as well as seasonal availability (Tennant 1984; Ernst and Ernst 2011). For example, in Kansas and Kentucky, mice and voles were the most frequently detected

prey (Bush 1959; Fitch 1982). We cannot exclude the possibility that some of the invertebrates may have been incidental prey originally consumed by the lizard prey of *A. contortrix* and the other snakes in this study. However, previous studies of Texas populations of *A. contortrix* have found that insects, especially cicadas, comprise a large proportion of the diet (Tennant 1984; Lagesse and Ford, 1996). Similarly, we observed that invertebrates were the most frequent prey consumed by *A. contortrix* from the WCGP (although due to their small size they may still represent a small proportion of prey biomass). However, we also did not detect any amphibians in the diet of *A. contortrix*, which may be

TABLE 2. The number of individual prey items (n), the numerical frequency of prey (%N), and the frequency of occurrence of prey items across individuals (%FO) found in stomach contents in three species of pitvipers from the West Gulf Coastal Plain of Texas and Louisiana, USA. N = the number of stomachs analyzed. Note: no *Sistrurus miliarius* stomachs were examined.

Taxon	<i>Agkistrodon contortrix</i> N = 2			<i>Agkistrodon piscivorus</i> N = 2			<i>Crotalus horridus</i> N = 10		
	n	%N	%FO	n	%N	%FO	n	%N	%FO
Invertebrates									
Unidentified insect	1	50	50	-	-	-	-	-	-
Aves									
Unidentified bird	-	-	-	-	-	-	1	10	10
Mammalia									
<i>Sylvilagus</i> sp.	-	-	-	-	-	-	1	10	10
<i>Peromyscus</i> sp.	-	-	-	-	-	-	1	10	10
<i>Sciurus carolinensis</i>	-	-	-	-	-	-	3	30	20
<i>Sciurus niger</i>	-	-	-	-	-	-	1	10	10
<i>Sciurus</i> sp.	-	-	-	-	-	-	1	10	10
Unidentified mammal	1	50	50	1	50	50	2	20	20
Reptilia									
<i>Virginia valeriae</i>	-	-	-	1	50	50	-	-	-

due to a potential lack of amphibian prey in the habitats where snakes were collected. However, amphibians also lack difficult to digest material such as scales, which may also be attributed to their absence from the fecal samples.

Agkistrodon piscivorus has been described as an opportunistic feeder that consumes a wide variety of ectothermic and endothermic prey (Ernst and Ernst 2011). However, while this species exhibits a broad range in prey items, Ernst and Ernst (2011) concluded that fish and amphibians are the most common prey items of *A. piscivorus*. Malloy (1971) found fishes to be a significant portion of cottonmouth diet at an eastern Texas fish hatchery, second only to frogs. As with the *A. contortrix* collected in this study, all of the *A. piscivorus* were collected in sites distant from aquatic habitats, which likely explains the lack of aquatic prey that is common in other dietary studies.

Most rattlesnake species exhibit a distinct ontogenetic shift in their diet from ectothermic to endothermic prey (Klauber 1972). Clark (2002) reviewed the diet of *C. horridus* across its range and observed its unusual affinity to specialize on endothermic prey across ontogeny. It was also observed that *C. horridus* do not drop smaller prey species from their diet as they grow, but rather expand their diet to include larger species (Clark 2002). Our results are consistent with other reports on the endothermic specialization of *C. horridus*. However, our results are not consistent with previous reports on the ontogenetic shifts by Clark (2002); rather than expand its diet to include large-bodied mammals during ontogeny, *C. horridus* individuals > 110 cm SVL did not consume small mammals (e.g., mice) as the diet of larger snakes consisted almost exclusively of larger mammals (*Sciurus niger*, *S. carolinensis*, and *Sylvilagus* spp). Southern (at least WGCP) populations of *C. horridus* reach substantially larger body sizes than northern populations, which may account for the deletion of smaller prey species from the diet.

Unlike *C. horridus*, which expands its diet preference to larger bodied-prey during ontogeny due to a larger skull size, *S. miliarius* is constrained by the size of prey that can be consumed due to its small skull size (Tennant 1984). Thus, the larger-bodied mammals (e.g., squirrels and rabbits) consumed by *C. horridus* are unavailable to *S. miliarius*. In our study, shrews and lizards

were the most frequently detected prey; their small body size likely makes them suitable prey for *S. miliarius*. Also unlike *C. horridus*, *S. miliarius* appears to exhibit no unusual affinity for strictly endothermic prey (Clark 1949, Hamilton and Pollack 1955, Ernst and Ernst 2011). The most frequently found prey items in individuals from Louisiana were frogs (Clark 1949) while small-bodied reptiles were found in 50% of the stomachs analyzed in Georgia, followed by centipedes (Hamilton and Pollack 1955). While, little is known on the feeding ecology of *S. miliarius* in Texas; Tennant (1984) reports anecdotal observations of *S. miliarius* preying upon Blanchard's Cricket Frog (*Acris blanchardi*) in the field and accepting tree frogs, chorus frogs, skinks, and captive mice in the lab. In a similar vein to the *A. piscivorus* collected in this study, *S. miliarius* were collected far from aquatic sites, which likely explains the absence of amphibians in the diet.

Fecal and stomach contents analysis provide greater resolution on the prey consumed, but are only a snapshot of recent prey items (Layman et al. 2015) and differential digestibility of prey affects detectability and evaluation of the importance of different prey (Litvaitis 2000). Stable isotopes are widely used in trophic and food-web studies (Pilgrim 2007, Willson et al. 2010, Layman et al. 2012, 2015). While results from stable isotope analysis lack the taxonomic resolution afforded from stomach contents or fecal analysis, it provides longer spatio-temporal insights into an organism's trophic ecology (Layman et al. 2012, 2015), which in turn, can provide insights to seasonal dietary shifts (*sensu* Willson et al. 2010) or response to environmental/ land use gradients (*sensu* Schalk et al. 2017). Our results would be complemented by future efforts that examine the trophic ecology of these snake species using stable isotope ratios, and provide insights into their feeding ecology across multiple spatio-temporal scales and environmental gradients.

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