

Variation in the Diet of *Sistrurus catenatus* (Massasauga), with Emphasis on *Sistrurus catenatus edwardsii* (Desert Massasauga)

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ABSTRACT.—We describe the diet of Desert Massasauga, *Sistrurus catenatus edwardsii*, in Arizona, Colorado, and New Mexico using fecal remains and gut contents obtained from field encounters and museum specimens. From these, 165 prey were identified, including 97 (58.8%) lizards, 51 (30.9%) mammals, 15 (9.1%) centipedes (*Scolopendra* sp.), one (0.6%) anuran, and one (0.6%) snake. Analyses of geographic, sexual and ontogenetic variation within *S. c. edwardsii* suggest diet is homogeneous among populations and between the sexes but that juveniles consume significantly more lizards and fewer mammals than adults. We assess rangewide variation in diet of *Sistrurus catenatus* using our data from Arizona, Colorado, and New Mexico (*S. c. edwardsii*) and previously published studies of populations in Wisconsin (*Sistrurus catenatus catenatus*), Michigan (*S. c. catenatus*), Missouri (*Sistrurus catenatus tergeminus*) and Texas (*S. c. tergeminus*) as well as new data from Texas (*S. c. tergeminus*). Significant geographic variation in diet parallels ecological and behavioral variation across the range of *S. catenatus*. *Sistrurus c. edwardsii* are xeric grassland-adapted snakes dependent on lizard and centipede prey, whereas both eastern subspecies favor more mesic environs and prey primarily on small mammals with juveniles occasionally feeding on snakes or lizards.

Recognizing and preserving biodiversity has become the primary goal of contemporary conservation biology. Recently, this objective has been most often pursued using molecular markers that illuminate patterns of diversity and corresponding evolutionary history. Although such approaches are important, if not critical, to managing imperiled taxa, they offer few insights to the ecological needs of the populations they delineate. Patterns of variability in natural history characters may or may not be concordant with evolutionary relationships among populations as revealed by molecular methods. Therefore, site-specific natural history studies that determine the conservation needs (e.g., feeding ecology, habitat requirements, etc.) of populations in the context of their biotic communities are essential. Another benefit of studying multiple populations of widespread organisms is that in the absence of molecularly based inferences, geographic patterns of variation in natural history characters can provide insights to possible phylogeographic scenarios, that can be tested subsequently using appropriate molecular methods. Regardless of concordance, evaluating patterns of variability in natural history characters relative to recovered phylogeny allows a broader understanding of evolutionary history (Greene, 1994) and the possible coevolution of character types.

The Massasauga (*Sistrurus catenatus*), found

from northern Chihuahua, Mexico, to southern Ontario, Canada, is threatened or endangered over much of its range and poses several interesting questions in phylogeography. Populations are highly fragmented (Gibbs et al., 1997) and there appear to be significant differences in natural history between Desert Massasauga (*Sistrurus catenatus edwardsii*) and other Massasauga populations. Although many aspects of the natural history of the Western Massasauga (*Sistrurus catenatus tergeminus*) and Eastern Massasauga (*Sistrurus catenatus catenatus*) have been researched (Wright 1941; Greene and Oliver, 1965; Keenlyne and Beer, 1973; Keenlyne, 1978; Reinert, 1981; Reinert and Kodrich, 1982; Seigel, 1986; Weatherhead and Prior, 1992; Johnson and Leopold, 1998; Seigel et al., 1998; Johnson, 2000), most aspects of the biology of *S. c. edwardsii* remain poorly studied (but see Hobert, 1997; Goldberg and Holycross, 1999). To conserve diversity within this group, a better understanding of population-specific variation in natural history is necessary (Greene, 1997).

Here we describe and compare diet of several populations of *S. c. edwardsii*, a form predominantly adapted to shortgrass prairies and desert grasslands but occasionally found in dune formations and desert scrub (Degenhardt et al., 1996). We also assess geographic variation in diet by comparing our results with quantitative studies of diet in populations of *S. c. catenatus* and *S. c. tergeminus*. Numerous anecdotal records (Appendix 1) and four studies (Greene and Oliver, 1965; Keenlyne and Beer, 1973; Sei-

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gel, 1986; Hallock, 1991) provide an extensive dataset on diet of the two eastern subspecies. In contrast, there are very few published, explicit prey records for *S. c. edwardsii*. Degenhardt et al. (1996) report a centipede (*Scolopendra* sp.) from the gut of a New Mexico specimen; Schwammer (1983) reports scavenging of a "grosse Maus" (big mouse) on a Colorado highway; and McKinney and Ballinger (1966) report *Uta* sp., unidentified lizard(s), and a centipede from four west Texas specimens. In addition, Hobert (1997) originally reported a portion of the data presented here (33 of our 58 Colorado records) in an unpublished master's thesis that was later summarized by Hammerson (1999).

MATERIALS AND METHODS

We sampled prey from *S. c. edwardsii* during parallel autecological investigations in Arizona (1993–1997) and Colorado (1995–1998). The Arizona population inhabits tobosa (*Hilaria mutica*) grassland that blankets a volcanic cinder field in the San Bernardino and San Simon Valleys, Cochise County. *Sistrurus c. edwardsii* is found in 11 counties in southeastern Colorado (Hammerson, 1999) in shortgrass prairie dominated by blue gramma (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*) growing on aridisols (Hobert, 1997). The majority (79%) of our Colorado prey records were collected from a single population in Lincoln County; remaining records were from Cheyenne (7%), Crowley (4%), and Kiowa (10%) Counties. We also collected samples from shortgrass prairie in the Rio Grande Valley, Valencia County, New Mexico (1997–1998). Although sampling efforts spanned April through October, in most years we emphasized late summer and fall sampling. We marked each live individual using passive integrated transponder tags (Jemison et al., 1995), recorded snout-vent length (SVL, mm) and mass (g), and determined sex by probing (Schaefer, 1934). We did not examine stomach contents of live snakes. Feces from live snakes (excreted voluntarily or palpated) and gut contents of DOR animals were preserved in 70% ethanol or 10% formalin and subsequently identified. In addition, we include data gathered from Arizona, Colorado, and New Mexico museum specimens (Appendix 2). Prey from specimens housed in captivity prior to preservation, or which appeared to have been fed in captivity (allopatric or domestic prey), were omitted. All museum specimens from Arizona and Colorado that contained prey originated from the populations discussed above. Museum specimens from New Mexico that contained prey were from the Rio Grande Valley ($N = 8$; Valencia, Bernalillo, Torrance, and Socorro Counties) or

Mescalero Sands ($N = 6$; Chaves and Lea Counties).

Lizard remains were identified to genus, and to species when possible, from whole remains or by using a dichotomous key we constructed based on diagnostic scale characters for resident lizards. When possible, small mammals were identified to genus using characteristics (gross morphology, medulla configuration, and scale patterns) of dorsal guard hairs (Moore et al., 1974). Centipedes (*Scolopendra* spp.) were identified from exoskeletal remnants of chelicerae, leg, or body segments. Snakes were identified from stomach remains or sections of skin found in the intestine. A single toad was identified to species.

For intrasubspecific statistical analyses, we grouped prey into three classes: lizards, small mammals, and centipedes. Two records, a snake and a toad, were excluded from analysis because they consisted of single observations. Rattlesnakes were divided into two length classes, juveniles (< 300 mm SVL) and adults (≥ 300 mm SVL) based on approximate minimum size for sexual maturity (280 mm males, 329 mm SVL females; Goldberg and Holycross, 1999).

For intersubspecific analyses, we compared diet data from these populations of *S. c. edwardsii* with data for *S. c. tergeminus* from Missouri (Seigel, 1986) and Texas (Greene and Oliver, 1965; this study) and *S. c. catenatus* from Michigan (Hallock, 1991) and Wisconsin (Keenlyne and Beer, 1973). We omitted low-frequency prey classes contributing zero values to cells and used an $R \times C$ test of independence to compare proportion of mammals versus squamates. Aside from the following exceptions, all data in these samples were collected from single populations. Our Colorado and New Mexico samples included a few samples from outside the focal population (see above). Hallock's (1991) sample was collected from museum specimens representing 17 counties in Michigan. Greene and Oliver's (1965) study included 21 prey identified from specimens collected in Parker and Tarrant counties and two additional records. We augmented Greene and Oliver's (1965) Texas sample of *S. c. tergeminus* by examining 161 specimens collected in the intervening years and deposited in the University of Texas at Arlington (UTA) collection (Appendix 2). These specimens yielded 88 additional prey records. Most prey were from Parker and Tarrant Counties ($N = 78$) with remaining prey records from Clay ($N = 1$), Haskell ($N = 1$), Hood ($N = 3$), Johnson ($N = 2$), Stonewall ($N = 1$), Throckmorton ($N = 1$), and Wilbarger ($N = 1$) Counties.

Statistics were computed using BIOMSTAT version 3.3 (F. J. Rohlf and D. E. Slice, Exeter Soft-

TABLE 1. Prey consumed by *Sistrurus catenatus edwardsii* in this study.

| Prey taxon | N | (%) |
|----------------------------------|-----|--------|
| Arthropoda | 15 | (9.1) |
| <i>Scolopendra</i> spp. | 15 | (9.1) |
| Anura | 1 | (0.6) |
| <i>Spea bombifrons</i> | 1 | (0.6) |
| Mammalia | 51 | (30.9) |
| <i>Baiomys taylori</i> | 1 | (0.6) |
| <i>Notiosorex crawfordi</i> | 3 | (1.8) |
| <i>Onychomys leucogaster</i> | 1 | (0.6) |
| <i>Perognathus</i> spp. | 1 | (0.6) |
| <i>Perognathus flavescens</i> | 8 | (4.9) |
| <i>Peromyscus</i> spp. | 1 | (0.6) |
| <i>Reithrodontomys megalotis</i> | 8 | (4.9) |
| Unidentified mammal | 28 | (17.0) |
| Squamata | 98 | (59.4) |
| <i>Tantilla nigriceps</i> | 1 | (0.6) |
| <i>Cnemidophorus</i> spp. | 6 | (3.6) |
| <i>Cnemidophorus sexlineatus</i> | 3 | (1.8) |
| <i>Cnemidophorus uniparens</i> | 25 | (15.2) |
| <i>Holbrookia maculata</i> | 20 | (12.1) |
| <i>Eumeces obsoletus</i> | 2 | (1.2) |
| <i>Sceloporus</i> spp. | 4 | (2.4) |
| <i>Sceloporus undulatus</i> | 29 | (17.6) |
| <i>Urosaurus ornatus</i> | 1 | (0.6) |
| <i>Uta stansburiana</i> | 2 | (1.2) |
| Unidentified lizard | 5 | (3.0) |
| Total | 165 | (100) |

ware, New York, 1999, unpubl.) or a pocket calculator. Means are reported \pm 1 SE. Nominal significance level was set at $\alpha = 0.05$ and Dunn-Sidak adjusted (Sokal and Rohlf, 1995) for multiple tests of the same dataset using the same test statistic (Cabin and Mitchell, 2000). Specifically, for four $R \times C$ tests of independence using all prey records $\alpha' = 0.013$. Parametric statistics were only applied to normally distributed data. Institutional abbreviations follow recommendations of Leviton et al. (1985).

RESULTS

In Arizona and New Mexico, we recorded 155 field encounters (captures + recaptures + DOR: 132 Arizona, 23 New Mexico) with 146 individual *S. c. edwardsii* (124 Arizona, 22 New Mexico). Seventy-one (63 Arizona, eight New Mexico) of these encounters yielded 84 identifiable prey (75 Arizona, nine New Mexico). In Colorado, 32 of 80 snakes encountered DOR (1995–1998) contained remains of 33 identifiable prey, and feces collected from 21 live specimens (1995–1996) yielded 23 prey. Twenty-three (36%) of 64 museum specimens examined (exclusive of those from our field work) yielded 25 identifiable prey (nine Arizona, two Colorado, 14 New Mexico).

From our three populations of *S. c. edwardsii*, we identified remains of 97 lizards (58.8%), 51 mammals (30.9%), 15 centipedes (9.1%), one

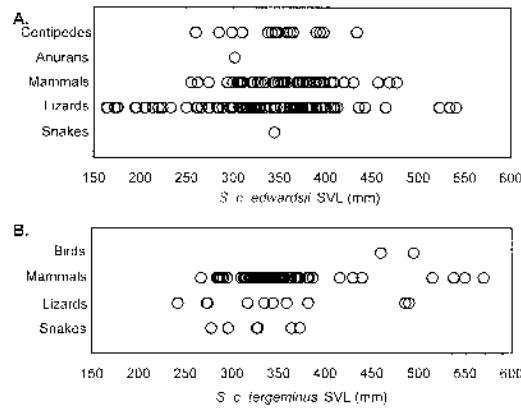


FIG. 1. Association between prey class and predator snout-vent length for (A) *Sistrurus catenatus edwardsii* from Arizona, New Mexico, and Colorado ($N = 163$), and (B) *Sistrurus catenatus tergeminus* from Texas ($N = 88$).

toad (0.6%, *Spea bombifrons*, Colorado) and one snake (0.6%, *Tantilla nigriceps*, central New Mexico). Identifications of lizards and mammals are provided in Table 1. All 15 centipedes were identified as *Scolopendra* spp., only four of which were found in a sample containing other prey remains. Judging by orientation in the stomach, six of eight centipedes were swallowed headfirst, whereas direction of ingestion could not be determined for two. All eighteen lizards found in stomachs were swallowed headfirst. We detected remains of two prey species in 16 snakes: lizard + mammal ($N = 7$), lizard + lizard ($N = 4$), centipede + mammal ($N = 3$), centipede + lizard ($N = 1$), and mammal + mammal ($N = 1$). One Arizona snake (ASU30149) contained three recently ingested lizards in its stomach (*Holbrookia maculata*, *Sceloporus undulatus*, and *Cnemidophorus uniparens*). Because we used prey remains from feces and the intestine (in addition to stomach contents), it is possible that snakes with multiple prey of the same prey-type were overlooked. Of the 165 *S. c. edwardsii* prey identified, 60 were identified from remains in the stomach and 105 from the colon or feces.

Predator SVL significantly differed among prey categories (Kruskal-Wallis test, $H_{(2)} = 7.90$, $P = 0.01$; Fig. 1A). Snakes that ate mammals were longest (mean SVL = 362 ± 7 mm, $N = 51$), followed in turn by those that fed on centipedes (349 ± 12 mm, $N = 15$) and lizards (329 ± 8 mm, $N = 95$). Snakes that fed on *Cnemidophorus* spp. ($N = 34$), *Sceloporus* spp. ($N = 33$) and *Holbrookia maculata* ($N = 19$) did not significantly differ in SVL (Kruskal-Wallis test, $H_{(2)} = 2.13$, $P = 0.34$). Juveniles and adults contained similar proportions of centipedes, but juveniles contained significantly more lizards and fewer

TABLE 2. Frequency of *Sistrurus catenatus edwardsii* prey classes by state, sex, age class, and sample type. One anuran and one snake are omitted (see text). Sample size for age class is lower ($N = 161$) than other comparisons ($N = 163$) because two specimens were not measured.

| | N | Centipedes N (%) | Lizards N (%) | Mammals N (%) |
|-----------|-----|---------------------|------------------|------------------|
| AZ | 84 | 5 (5.6) | 54 (64.3) | 25 (29.8) |
| CO | 57 | 3 (5.3) | 31 (54.4) | 23 (40.4) |
| NM | 22 | 7 (31.8) | 12 (54.6) | 3 (13.6) |
| Males | 95 | 8 (8.4) | 53 (55.8) | 34 (35.8) |
| Females | 68 | 7 (10.3) | 42 (61.8) | 19 (27.9) |
| Juveniles | 36 | 3 (8.3) | 29 (80.6) | 4 (11.1) |
| Adults | 125 | 12 (9.6) | 66 (52.8) | 47 (37.6) |
| Colon | 58 | 8 (13.8) | 38 (65.5) | 12 (20.7) |
| Stomach | 105 | 7 (6.7) | 59 (56.2) | 39 (37.1) |

mammals ($G_{\text{Williams}} = 10.8$, $df = 2$, $P < 0.01$; Table 2). Diet was independent of sex ($G_{\text{Williams}} = 0.7$, $df = 2$, $P = 0.70$; Table 2) and source (stomach vs. colon/feces) of sample ($G_{\text{Williams}} = 5.8$, $df = 2$, $P = 0.06$; Table 2). Centipedes and mammals appear to be taken more frequently later in the foraging season (Fig. 2). Proportion of prey classes consumed by *S. c. edwardsii* differed among populations ($G_{\text{Williams}} = 14.0$, $df = 4$, $P = 0.007$; Table 2). However, all pairwise comparisons (AZ-CO, AZ-NM, CO-NM) between populations comprised nonsignificant subsets ($G = 1.7, 10.3, 11.7$, respectively) of this analysis. The small New Mexico sample contained proportionately more centipedes and fewer mammals than the other two samples (Table 2).

From the Texas *S. c. tergeminus*, we identified remains of 70 mammals (79.5%), 10 lizards (11.4%), 6 snakes (6.8%), and 2 birds (2.3%). Mammals consisted of 39 soricids (four identified as *Cryptotis parva*), 13 cricetids, 2 heteromyids (*Perognathus* spp.), 1 geomyid, and 15 unidentified. Lizards consisted of five *Cnemidophorus* spp. and five unidentified skinks. One snake was identified as *Tropidoclonion lineatum*. We detected remains of two prey species in five snakes: mammal + mammal ($N = 2$), snake + mammal ($N = 2$), and lizard + mammal ($N = 1$).

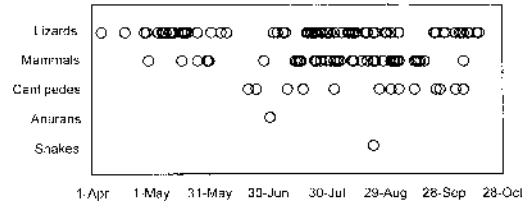


FIG. 2. Seasonal distribution of prey consumed by *Sistrurus catenatus edwardsii* ($N = 165$).

Orientation of prey remains in the stomach suggested that 18 mammals, three *Cnemidophorus* spp., three skinks (identified from tails in the stomach), two snakes, and one bird were consumed headfirst, whereas one mammal was consumed rump first. Proportion of prey classes for this population as well as other previously published diet studies of the two eastern subspecies are provided in Table 3.

In comparisons among subspecies, we found that proportion of mammals versus squamates was dependent on source population ($G_{\text{Williams}} = 120.8$, $df = 6$, $P \approx 0$). The Michigan, Missouri, and Wisconsin samples composed a nonsignificant subset of this analysis ($G = 4.3$), as did the Arizona, Colorado, and New Mexico samples ($G = 3.3$). Interestingly, the Michigan, Missouri, and Texas populations also composed a nonsignificant subset ($G = 1.9$). Snake SVL did not significantly differ between *S. c. edwardsii* (pooled) and *S. c. tergeminus* (our sample from Texas) that ate squamates (ANOVA, $F_{1,110} = 0.35$, $P = 0.56$) or mammals (ANOVA, $F_{1,119} = 0.89$, $P = 0.35$). Nevertheless, proportion of squamates vs. mammals consumed by 300–400 mm SVL *S. c. edwardsii* and 300–400 mm SVL *S. c. tergeminus*

TABLE 3. Relative occurrence of *Sistrurus catenatus* prey class by population. Arizona (AZ), Colorado (CO), and New Mexico (NM) populations are *Sistrurus catenatus edwardsii*, Texas (TX) and Missouri (MO) populations are *Sistrurus catenatus tergeminus* and Michigan (MI) and Wisconsin (WI) populations are *Sistrurus catenatus catenatus*.

| | Mammals | | Lizards | | Snakes | | Centipedes | | Other | | Source |
|----|---------|-----------|-----------|-----|----------|-----|------------|-----|---------|-----|--|
| | N | N (%) | N | (%) | N | (%) | N | (%) | N | (%) | |
| AZ | 84 | 25 (29.8) | 54 (64.3) | | 0 | | 5 (6.0) | | 0 | | This study |
| CO | 57 | 23 (39.7) | 31 (53.5) | | 0 | | 3 (5.2) | | 1 (1.7) | | This study |
| NM | 22 | 3 (13.0) | 12 (52.2) | | 1 (4.4) | | 7 (30.4) | | 0 | | This study |
| MO | 20 | 16 (80.0) | 0 | | 4 (20.0) | | 0 | | 0 | | Seigel, 1986 |
| TX | 111 | 81 (73.0) | 15 (13.5) | | 11 (9.9) | | 0 | | 4 (3.6) | | Greene and Oliver, 1965 ($N = 23$); This study ($N = 88$) |
| MI | 43 | 33 (76.4) | 0 | | 6 (14.0) | | 0 | | 4 (9.3) | | Hallock, 1991 |
| WI | 96 | 85 (93.4) | 0 | | 5 (5.5) | | 0 | | 1 (1.1) | | Keenlyne and Beer, 1973 |

from Texas was dependent on subspecies ($G_{\text{wilhams}} = 31.9$, $df = 1$, $P < 0.01$; Fig. 1).

DISCUSSION

Based on a few records from *S. c. catenatus* (Appendix 2), several early works erroneously suggested that frogs are prominent in the diet of *S. c. catenatus* (Ditmars, 1912; Evermann and Clark, 1914; Pope, 1926; Ruthven et al., 1928), an assertion later reiterated by Wright and Wright (1957) and Klauber (1972). Subsequent quantitative studies (see Table 3) suggest that, although anurans are preyed upon, they are not consumed in abundance by any subspecies of *S. c. catenatus*.

These early reports on eastern subspecies may have led Fowlie (1965) to state that *S. c. edwardsii* feed primarily on amphibians. Although Fowlie based his conclusion on "examination of stomach contents," he neither cited a source nor referenced specimens. Despite the paucity of published prey records for *S. c. edwardsii*, several authors (Lowe et al., 1986; Greene, 1997) correctly postulated a diet consisting primarily of mice and lizards but did not provide data. Several regional field guides (Stebbins, 1985; Bartlett and Tennant, 2000) listed mice and lizards as food of *S. c. edwardsii*, but still included frogs, and failed to mention centipedes, as important components of diet. Our data demonstrate lizards are the modal prey of *S. c. edwardsii*, although small mammals and centipedes also comprise significant proportions of the diet.

Although *S. c. catenatus* appears to consume anurans infrequently, Werler and Dixon (2000) suggested toads may "constitute an important part of the Massasauga's diet when they are available" based on *S. c. catenatus*' large adrenal glands (Smith and White, 1955). In other ophidians, enlarged adrenals apparently relate to a diet of toads (Smith and White, 1955), many of which have toxic skin-gland secretions containing epinephrine and digitaloid compounds. Interestingly, this speculation was based on examination of the adrenal glands of *S. c. catenatus* (Smith and White, 1955) for which there are records of frog (but not toad) consumption (Appendix 2). Certainly both bufonid and pelobatid toads are a syntopic and seasonally abundant potential food source throughout the range of *S. c. edwardsii*. However, the majority of our specimens were collected during rainy seasons when toads were surface-active and abundant, yet we documented only a single toad among the 60 prey identified from stomach contents.

Lizards comprise a surprisingly large proportion of the adult diet of *S. c. edwardsii* relative to the diet of conspecifics and to the prevalence of mammals in the diet of many northern pit vi-

pers (Mushinsky, 1987; Ernst, 1992). Ontogenetic shifts in diet account for prevalence of lizards in the diet of some rattlesnakes (e.g., Mackessy, 1988; Holycross et al., in press) but only partially explain their prevalence in the diet of *S. c. edwardsii*. Clearly, *S. c. edwardsii* < 250 mm SVL feed exclusively on lizards, probably because these snakes are physically incapable of ingesting even small rodents. However, squamates (lizards) are consumed 1.5 times more often than mammals even after these gape-limited predators exceed 300 mm SVL and begin to consume a variety of small mammals (Fig. 1A).

The high number of solitary centipede records suggests directed foraging on live centipedes rather than secondary ingestion or scavenging. Large centipedes are not uncommon in the diets of *Sistrurus miliaris* (Hamilton and Pollack, 1955), *Crotalus enyo* (Taylor, 2001), *Crotalus willardi obscurus* (Holycross et al., in press), and *Crotalus lepidus klauberi* (ATH, unpubl. data). Although foraging behaviors associated with mammalian prey have been studied extensively, little is known of how rattlesnakes forage on centipedes. Nevertheless, it seems likely that centipede-eaters have evolved specific adaptations for foraging on this fractious and venomous prey. For example, Rubio (1998) wondered if centipede-eaters are resistant to centipede venom. Several observations suggest centipede-specific prey-handling behaviors in *C. lepidus*, *C. willardi*, and *S. c. edwardsii* (Rubio, 1998; H. McCrystal, pers. comm.; D. Sias, pers. comm.). Regardless of how centipedes are envenomated and handled, our few observations hint that *S. c. edwardsii* usually ingests them headfirst.

Diet of the three *S. c. edwardsii* populations is essentially homogeneous in both intra- and intersubspecific comparisons. Not only do *S. c. edwardsii* populations consume similar proportions of broadly defined taxa, but they also consume many of the same prey genera and species (e.g., *H. maculata*, *S. undulatus*, *Cnemidophorus* spp.). Likewise, Wisconsin and Michigan *S. c. catenatus* and Missouri *S. c. tergeminus* populations all consume similar proportions of mammals versus squamates and consume similar prey genera. Thus, similarities within and differences among the diet of these eastern and western groups are not limited to proportion of mammals versus squamates consumed but extend to the taxa of mammals and squamates consumed. Populations in Arizona, Colorado, and New Mexico appear to rely primarily on harvest mice (*Reithrodontomys* spp.) and pocket mice (*Perognathus* spp.), whereas Michigan, Wisconsin, and Missouri populations rely chiefly on voles (*Microtus* spp.) and shrews (*Blarina* spp. and *Sorex* spp.) and occasionally jumping mice (*Zapus* spp.). Correspondingly, Arizona, Colorado, and

New Mexico (*S. c. edwardsii*) populations rely heavily on lizards and rarely eat snakes, whereas snakes are the only squamates documented in the diet of Michigan, Wisconsin, and Missouri populations and were usually consumed by juveniles (Keenlyne and Beer, 1973; Seigel, 1986; Hallock, 1991). The Texas population of *S. c. tergeminus* did not significantly differ from the Michigan and Missouri populations in proportion of mammals versus squamates consumed and likewise consumed a high proportion of shrews. Infrequent consumption of ranid frogs and the absence of centipedes also suggest primary dietary affiliations with eastern populations. The Texas sample of squamates consisted of similar proportions of snakes and lizards (Table 3). Hence, the Texas population appears intermediate between the divergent diets of eastern and western groups but appears to have more commonalities with eastern diets.

Differences in diet among populations of *S. c. edwardsii*, *S. c. tergeminus*, and *S. c. catenatus* parallel other ecological and behavioral differences. *Sistrurus c. edwardsii* inhabit dry grasslands and dune formations (Stebbins, 1985; Degenhardt et al., 1996; Hammerson, 1999), whereas *S. c. tergeminus* and *S. c. catenatus* typically inhabit wet grasslands, marshes, swamps, and small meadows in woodlands (Seigel, 1986; Reinert and Kodrich, 1982; Weatherhead and Prior, 1992). Prey of eastern subspecies are generally associated with mesic habitats (Appendix 2), whereas *S. c. edwardsii* prey are associated with xeric grassland communities (Table 1). *Sistrurus c. tergeminus* in Parker and Tarrant Counties, Texas, occupy intermediate habitat described as "gently rolling, tall grass prairie, interrupted by an occasional shallow creek or rocky hillside" (Greene and Oliver, 1965).

Clearly, geographic variation in prey availability and clinal variation in size (with eastern forms larger than western forms) account, in part, for geographic variation in diet. Lizards and large centipedes are not abundant in the habitat of some eastern populations, and larger size allows eastern subspecies to consume a wider size-range of small mammals. However, *S. c. edwardsii* and *S. c. tergeminus* that ate the same prey class (mammals or squamates) did not significantly differ in SVL. In this comparison, size alone does not account for the significant disparity in proportion of prey classes consumed. The Texas sample of *S. c. tergeminus* > 300 mm SVL consumed mammals 5.5 times more often than squamates (Fig. 1B), despite the presence of a fairly abundant lizard fauna. Conversely *S. c. edwardsii* > 300 mm SVL consumed squamates 1.5 times more often than mammals (Fig. 1A), despite a diverse and abundant rodent fauna at all three field sites. Thus, differ-

ences in diet may also reflect foraging adaptations to different prey communities rather than opportunism alone, as suggested by studies of the stimulus-control of foraging behaviors. For example, Schuett et al. (1984) reported that captive juvenile *S. c. catenatus* caudal lure for frogs and Reiserer (in press) reported that captive juvenile *S. c. tergeminus* from Kansas caudal lure for frogs but not lizards. Conversely, Reiserer (in press) reported that juvenile *S. c. edwardsii* from Arizona caudal lure for lizards but not frogs. Reiserer's experiments suggest the primary stimulus-control is prey movement patterns. Analysis of venom proteins from Arizona, Colorado, Kansas, Missouri, New Mexico, and Wisconsin populations group *S. c. edwardsii* separate from conspecific subspecies (R. W. Milne and S. P. Mackessy, unpubl.). Venom from *S. c. edwardsii* is also consistently more toxic (to inbred lab mice, and presumably to lizards) than venom from the two eastern subspecies (SPM, unpubl. data). The evolution of a switch in stimulus-control of a foraging behavior and differences in venom profiles among subspecies suggest adaptation to different prey communities. Other aspects of foraging ecology may have undergone similar adaptive radiation. Rattlesnakes rely heavily on chemical cues when selecting ambush sites. *Sistrurus miliarius barbouri* prey primarily on frogs and select foraging sites based on the presence of frog odors (Roth et al., 1999), whereas *Crotalus viridis viridis* select sites based on the presence of rodent olfactory cues (Duvall et al., 1990a,b). We imagine that experiments examining foraging site selection by *S. c. catenatus* using different prey odors would yield patterns (among subspecies) similar to Reiserer's experiments on stimulus-control for caudal luring.

Although the precise pattern and tempo of these evolutionary changes is unclear, paleoecological evidence considered in light of extant patterns in natural history offers intriguing insights. Fossil remains from the middle and late Pliocene (Kansas, Nebraska, and Texas) and the middle Pleistocene (Kansas and Nebraska) suggest *S. c. catenatus* was present over much of its current range in the Great Plains both prior to and during Pleistocene glacial oscillations (Holman, 2000). Schmidt (1938) argued that most of the range of *S. c. catenatus* is the product of an eastward expansion across the "prairie peninsula" of the Great Lakes region following the retreat of the Wisconsinan Laurentide Ice Sheet. However, a fossil *S. c. catenatus* from eastern West Virginia (Holman, 2000) precedes the Laurentide Ice Sheet by approximately 300,000 yr or more and raises the possibility that during the Wisconsinan an isolated group of *S. c. catenatus* persisted southeast of the ice sheet. Thus, a

deeper divergence may separate western forms from their eastern relatives and occupation of the "prairie peninsula" may not have originated from the west alone. Regardless of intraspecific phylogeny, *S. c. catenatus* and *S. c. tergeminus* appear to have retained adaptations to pluvial communities, whereas populations of *S. c. edwardsii* appear to have derived adaptations to xerification of western habitats and prey communities during the Holocene. Pluvial communities in the southwest probably approximated modern conditions for *S. c. tergeminus* and *S. c. catenatus* in that the region was wetter and cooler. Indeed, the most southwestern populations of *S. c. edwardsii* persist in desert grasslands devoid of microtine rodents, yet as recently as approximately 4000–9000 yr ago this area supported mesic grasslands and lakeshores that teemed with microtines (Van Devender and Worthington, 1977; Van Devender, 1995). If populations of *S. c. edwardsii* were isolated from one another early in this history they may have convergently derived adaptations to xerification and new prey communities (e.g., stimulus-control of feeding responses, venom characteristics, habitat use, body size and its correlates).

Until a better understanding of this group's phylogeography is achieved, prudent conservation practices will recognize the uniqueness of *S. c. edwardsii* and afford it separate status in risk assessment and management. These populations currently depend on open grassland habitats that support a fauna of grassland lizards, large centipedes, and small mammals. Management practices that negatively affect these communities and/or prey species will undoubtedly negatively affect *S. c. edwardsii*. Desertification (anthropogenic by definition) and the spread of agriculture have already led to the extirpation of populations in Arizona (Lowe et al., 1986).

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APPENDIX 1. Summary of original records for prey of *Sistrurus catenatus catenatus* and *Sistrurus catenatus tergeminus*. An asterisk denotes prey consumed in captivity. As cited in (a) Klauber, 1972 and (b) Wright, 1941.

| Prey | Reference |
|---|---|
| Arthropoda | |
| "insect" | Hallock, 1991 |
| "crayfish" | Allen (pers. comm. in Reinert, 1978) |
| <i>Scolopendra</i> spp. | Lardie, 1976 |
| Anura | |
| Unidentified frog | Ruthven, et al., 1928; Pope, 1926; Netting, 1932; Fox, 1948 ^a |
| Unidentified frog* | Ditmars, 1907; Atkinson and Netting, 1927; Curran, 1935 |
| <i>Acris crepitans</i> | Reiserer, in press |
| <i>Hyla crucifer</i> (<i>Pseudacris crucifer</i>) | Atkinson and Netting, 1927; Netting, 1932 |
| <i>Rana</i> spp. | LeRay, 1930; Netting 1932; Hallock, 1991 |
| <i>Rana berlandieri</i> | Greene and Oliver, 1965 |
| <i>Rana clamitans</i> * | Schuetz et al., 1984 |
| <i>Rana pipiens</i> * | Schuetz et al., 1984 |
| <i>Rana sylvatica</i> * | Schuetz et al., 1984 |
| Aves | |
| "bird" | Netting, 1932; Hallock, 1991; This study |
| "bird" | Ditmars, 1907 |
| "sparrows"* | Selous, 1900; Loewen, 1947 ^a ; Best, 1978 |
| "chicks"* | Loewen, 1947 ^a |
| "warbler" | Minton, 1972 |
| <i>Agelaius phoeniceus</i> | Keenlyne and Beer, 1973 |
| <i>Chondestes grammacus</i> (eggs) | Brush and Ferguson, 1986 |
| <i>Colinus virginianus</i> (eggs) | Applegate, 1995 |
| <i>Melospiza melodia</i> | Weatherhead and Prior, 1992 |
| Mammalia | |
| Unidentified mammal | Taylor, 1892; Greene and Oliver, 1965; Seigel, 1986; Hallock, 1991; This study |
| "rodent" | Hallock, 1991 |
| "mice" | Taylor, 1892; Netting, 1932; Conant 1951 |
| "mice"* | Selous, 1900; Ditmars, 1907; Swanson, 1930; LeRay, 1930; Wright, 1941; Loewen, 1947 ^a ; Conant, 1951; Adler, 1960; Keenlyne, 1968; Johnson, 1995 |
| "rabbit,"* "bat,"* "mole"* | Loewen, 1947 ^a |
| "cricketid" | This study |
| "microtine" | Reinert, 1978; Hallock, 1991 |
| "geomyid" | This study |
| "soricid" | This study |
| "zapodid" | Hallock, 1991 |
| <i>Blarina</i> spp. | Johnson, 1995 |
| <i>Blarina brevicauda</i> | Green and Oliver, 1965; Reinert, 1978; Hallock, 1991; Mauder and Wilson, 1999 |
| <i>Clethrionomys gapperi</i> | Hallock, 1991 |
| <i>Cryptotis parva</i> | This study |
| <i>Sorex</i> spp. | Johnson, 1995 |
| <i>Sorex cinereus</i> | Keenlyne and Beer, 1973; Anton, 1993 |
| <i>Lepus americanus</i> | Weatherhead and Prior, 1992 |
| <i>Microtus</i> spp. | Crawford, 1936; Lyon and Bishop, 1936; Wright, 1941; Mauder and Wilson, 1999; Hallock, 1991 |
| <i>Microtus ochrogaster</i> | Siegel, 1986 |
| <i>Microtus pennsylvanicus</i> | Atkinson and Netting, 1927; Lyon and Bishop, 1936; Conant, 1951; Keenlyne and Beer, 1973; Hallock, 1991 |
| <i>Napaeozapus insignis</i> | Hallock, 1991 |
| <i>Perognathus</i> spp. | This study |
| <i>Perognathus hispidus</i> | Greene and Oliver, 1965 |
| <i>Perognathus merriami</i> | Greene and Oliver, 1965 |
| <i>Peromyscus</i> spp. | Seigel, 1986; Mauder and Wilson, 1999; Johnson, 1995; Hallock, 1991 |
| <i>Peromyscus leucopus</i> | Wright, 1941; Keenlyne and Beer, 1973; Reinert, 1978 |
| <i>Reithrodontomys montanus</i> | Greene and Oliver, 1965 |
| <i>Zapus hudsonius</i> | Bielema, 1973; Keenlyne and Beer, 1973; Johnson, 1995 |

APPENDIX 1. Continued.

| Prey | Reference |
|---|---|
| Squamata | |
| Unidentified snake | Ruthven et al., 1928; Conant, 1951; Greene and Oliver, 1965; Keenlyne and Beer, 1973; Hallock, 1991; This study |
| <i>Heterodon nasicus</i> | Greene and Oliver, 1965 |
| <i>Opheodrys vernalis</i> | Mauger and Wilson, 1999 |
| <i>Sistrurus catenatus</i> | Ruthven, 1911 ^b ; Hallock, 1991 |
| <i>Sistrurus catenatus</i> * | Keenlyne, 1968 |
| <i>Sonora episcopa</i> (= <i>semiannulata</i>) | Greene and Oliver, 1965 |
| <i>Storeria dekayi</i> | Seigel, 1986; Mauger and Wilson, 1999 |
| <i>Storeria dekayi</i> * | Johnson, 1995 |
| <i>Storeria occipitomaculata</i> | Reinert, 1978 |
| <i>Thamnophis</i> spp. | Hallock, 1991 |
| <i>Thamnophis radix</i> * | T. Anton, pers. comm. |
| <i>Thamnophis sirtalis</i> | Keenlyne and Beer, 1973; Seigel, 1986 |
| <i>Thamnophis sirtalis</i> * | Keenlyne, 1968 |
| <i>Tropidoclonion lineatum</i> | Greene and Oliver, 1965; This study |
| <i>Cnemidophorus</i> spp. | Klauber, 1972; This study |
| <i>Cnemidophorus</i> spp.* | Loewen, 1947 ^a |
| <i>Cnemidophorus gularis</i> | Greene and Oliver, 1965 |
| <i>Crotaphytus collaris</i> | Webb, 1970 |
| <i>Crotaphytus collaris</i> * | Loewen, 1947 ^a |
| Unidentified skink | This study |
| <i>Lygosoma laterale</i> (<i>Scincella lateralis</i>) | Greene and Oliver, 1965 |
| <i>Phrynosoma cornutum</i> | Greene and Oliver, 1965 |
| <i>Sceloporus olivaceus</i> | Greene and Oliver, 1965 |

APPENDIX 2.

Museum specimens examined. *Abbreviations.*—American Museum of Natural History (AMNH), Arizona State University (ASU), Museum of Southwestern Biology (MSB), Museum of Vertebrate Zoology (MVZ), University of Arizona (UAZ), University of Colorado Museum (UCM) and University of Northern Colorado Natural History Museum (UNC-MNH). AMNH 107537; ASU 30148–51, 30153–71, 30577–92, 30621–38, 30877, 30899–906, 32947; MSB 04752, 05232, 17805, 19811, 22091–92, 24362, 30927, 30928, 32059, 32381, 34658, 37967, 41681, 42754, 51881, 51941–42, 52129, 52737, 52891, 52893–94, 53027, 53336, 53913, 54112, 54414, 54904, 55142, 55162–63, 56032, 56286, 56411–12, 56580, 56660, 56663, 56673, 56689–90,

56872, 58680, 59510–11, 60589, 60803–05, 61102, 61228, 61364; MVZ 79231, 209129, 226244; UAZ 45477, 45668; UCM 42373; UNC-MNH 90, 150, 226, 249, 282, 375, 404, 412, 417, 440–42, 450, 494–502, 504–511, 514, 516, 529, 563–64, 568, 575, 601–06, 631, 635, 641, 656, 726, 727, 747, 769, 770, 778–79, 799, 800–01, 816–19, 824–25, 832, 886, 923, 927, 930, 934–35, 938, 968, 971, 977, 983–85, 1004, 1009, 1010, 1044, 1453–54, 1492, 2244; UTA 2902, 2904–05, 9048, 9296, 10996–97, 11279–367, 12676–684, 14081–83, 16393, 19344–45, 19347, 19468, 22372–76, 24518–19, 26538, 28804–09, 30455, 30851–52, 31406, 32386–391, 32397, 32433–35, 32593, 33675, 33777–78, 33955, 34138, 34607, 34703, 34763–64, 34904, 35391, 38806, 38871, 40361–62, 40668, 40817, 40829–839, 40851–52.