FORAGING ECOLOGY OF THE THREATENED NEW MEXICO RIDGE-NOSED RATTLESNAKE (*CROTALUS WILLARDI OBSCURUS*)

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Abstract: We describe the diet of the New Mexico Ridge-nosed Rattlesnake (*Crotalus willardi obscurus*) throughout its range, using fecal remains and stomach contents obtained from 317 encounters with 246 individuals and a single literature record. Eighty-nine of 317 encounters (28.1%) yielded 95 identifiable prey items. Diet was independent of geographic distribution (mountain range), sex, and season. Juvenile diet consisted primarily of lizards (57.1%) and centipedes (33.3%), and adults fed primarily on small mammals (62.3%), lizards (26.4%), and occasionally passerine birds (9.4%). Brush mice (*Peromyscus* spp.) constituted 64.9% of rodents consumed and *Sceloporus* spp. accounted for 68.4% of lizards. *Peromyscus boylii* and *S. jarrovii* were most abundant in pine-oak woodland and talus habitats frequented by *C. w. obscurus*. Radiotagged adult *C. w. obscurus* were often found in ambush postures along fallen branches and at the base of partially-felled trees used as runways by *P. boylii*. Preservation of mature woodland is recommended for long-term persistence of *C. w. obscurus* and its prey.

Introduction

Predator-prey interactions are widely recognized as primary influences in snake evolution (Greene, 1983; Mushinsky, 1987). Selective pressures as they relate to diet affect morphology (Arnold, 1993, Forsman and Shine, 1997), physiology (Secor and Diamond, 1998), community structure (Reynolds and Scott, 1982; Vitt, 1983; Rodríguez-Robles and Greene, 1996), movement/activity patterns (Duvall et al., 1990; Secor, 1995; Madsen and Shine, 1996) and habitat use (Reinert et al., 1984; Chandler and Tolson, 1990). Ontogenetic, sexual, or geographic differences in diet may reflect associated variation in other aspects of autecology and/or phylogeographic history. Thus, dietary assays can provide valuable insights into the evolution of natural and life history characters (Shine, 1996; Rodríguez-Robles et al., 1999) and may have significant implications for conservation of imperiled populations (e.g., Downes and Shine, 1998; Shine et al., 1998). Unfortunately, data are often lacking or difficult to obtain for endangered species, particularly those that are secretive.

Here we describe and evaluate the foraging ecology of the federally threatened (U. S. Fish and Wildlife Service, 1978) New Mexico Ridge-nosed Rattlesnake (*Crotalus willardi obscurus*) and discuss autecological insights and implications for conservation. *Crotalus willardi* is presumed to be "predominantly adapted to montane pine-oak woodlands" of the Sierra Madre Occidental (McCranie and Wilson, 1987), though its niche in this community is poorly understood. *Crotalus w. obscurus* is restricted to three isolates, inhabiting the Animas Mountains (New Mexico, USA), Peloncillo Mountains (Arizona and New Mexico, USA) and Sierra San Luis (Sonora and Chihuahua, Mexico). Prior to this study, a single natural prey record existed for this subspecies (Marshall, 1957), although a portion of the data we present were summarized in Degenhardt et al. (1996).

MATERIALS AND METHODS

Individuals of *C. w. obscurus* were sampled throughout the species' range during an investigation of its autecology and conservation biology. Mark-recapture sampling took place in the Animas Mountains (1990 to 1991, and 1993 to 1999), Peloncillo Mountains (1995 to 1998), and Sierra San Luis (1988 to 1989, and 1998). Observations of foraging behavior were effected through unobtrusive daily monitoring of radiotagged snakes in the Animas Mountains (1994 to 1996, and 1999) and Peloncillo Mountains (1997). Although sampling spanned April through October, in most years it was restricted to late summer and fall (July and August). We marked each individual using passive-integrated transponder (PIT) tags (Jemison et al., 1995), recorded snout-vent length (mm) and mass (g), and determined sex by probing (Schaefer, 1934). We attempted to collect fecal samples from all snakes, regardless of whether remains were detected in the colon, by gently massaging the distal abdomen in the direction of the vent. Fecal material was preserved in 70% ethanol or 10% formalin for subsequent identification. Presence or absence of prey in the stomach was determined by palpation. Rarely, stomach contents were gently massaged to the mouth

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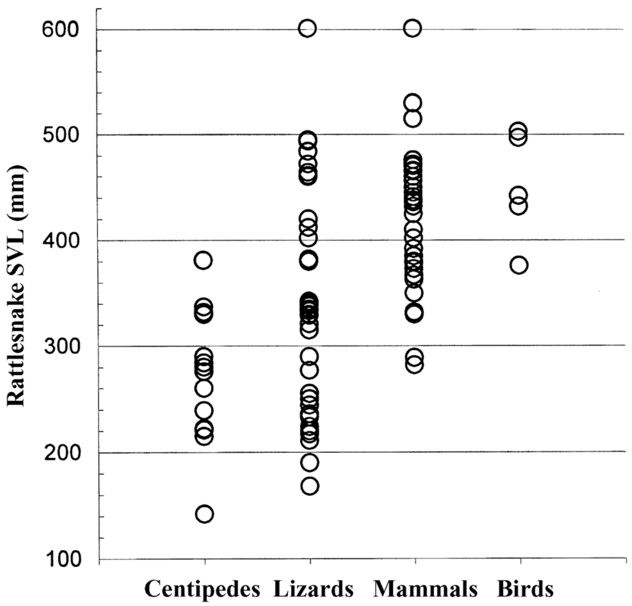

Fig. 1. Association between prey class and predator (*Crotalus willardi obscurus*) snout-vent length (SVL). N = 95.

of the snake for identification, and returned to the stomach by the same method. We did not attempt to identify stomach contents if injury to the snake seemed possible based on predator/prey size ratio or presumed type of prey (e.g. *Sceloporus* spp. which are usually ingested head-first due to orientation of their spiny scales). Lizard remains were identified to genus and species (when possible), using a dichotomous key based on diagnostic scale characters for resident lizards. 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. Birds were identified from diagnostic primary flight feathers and tarsi. Also included in our analyses is a specimen (UAZ 27943) collected in the Sierra San Luis on 3 September 1952 (Marshall, 1957).

A survey of the small mammal community at the Animas Mountain site (ca. 2,100–2,600 m elevation) was conducted on 16 nights in July and August 1996. Sherman live-traps baited with oatmeal/birdseed mixture were concurrently set in lines of 25 traps each in four habitats: pine-oak woodland (*Pinus engelmanni*, *P. strobiformis*, *Pseudotsuga menziesii*, and *Quercus gambelli*), encinal (*sensu* Lowe, 1967:52–53; *Juniperus deppeana*, *P. cembroides*, *Q. arizonica*, *Q. emoryi*, and *Q. hypoleucoides*), talus slope (*Q. rugosa* and *Robinia neomexicana*, interspersed) and grass-dominated plateau (*Eragrostis intermedia*, *Bouteloua gracilis*, and *Muhlenbergia trifida*). The total trapping effort equaled 1,600 trap-nights.

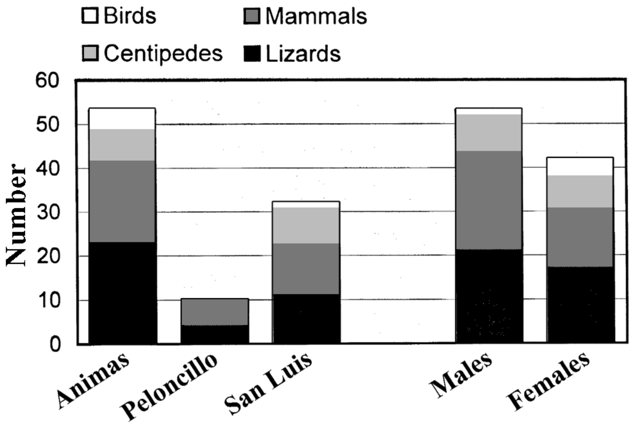

Fig. 2. Distribution of *C. willardi obscurus* prey classes among three mountain populations and between the sexes.

For statistical analyses, we grouped prey into four classes: small mammals, birds, lizards, and centipedes. We divided snake foraging season into two periods, dry season (18 April to 15 July) and wet season (16 July to 24 October). Snakes < 350 mm in snout-vent length (SVL) are referred to as juveniles, and animals ≥ 350 mm SVL are referred to as adults. Holycross and Goldberg (2001) report that the smallest reproductive male examined measured 406 mm SVL, the smallest pregnant female measured 402 mm SVL, and several females < 425 mm SVL were pregnant. Pregnant females in these populations are in the second year of their first reproductive cycle (Holycross and Goldberg, 2001). Given this evidence and the relatively small sample of histological examinations, we conclude it reasonable to assume that free-living animals reach reproductive maturity between 350 and 400 mm SVL.

Statistics were computed using BIOMstat version 3.3 (Rohlf and Slice, 1999). Significance level for individual tests was Bonferroni adjusted where appropriate. Institutional abbreviations are as listed in Leviton et al. (1985).

RESULTS

Individuals with radiotransmitters were observed on 1,951 occasions during the course of the study. There were 317 encounters (captures + recaptures: 230 Animas, 69 San Luis, 18 Peloncillo) involving 246 individuals of *C. w. obscurus* (160 Animas, 69 San Luis, 17 Peloncillo). Eighty-nine of 317 encounters (28.1%) yielded 95 identifiable prey items, 88 from feces and seven from stomach contents. Five fecal samples contained remains of two prey species, and one individual contained prey in its stomach and feces. Three individuals contained identifiable prey on two separate encounters. Presence/absence of prey was independent of sex ($G = 1.21$, $df = 1$, $P = 0.271$), but dependent on length class ($G = 5.04$, $df = 1$, $P = 0.025$); juveniles contained prey more frequently (34.5%) than adults (24.4%).

Small mammals (38.9%) and lizards (40.0%) comprised the majority of prey consumed (Table 1). *Peromyscus* spp. constituted 64.9% of rodents consumed and *Sceloporus* spp. accounted for 68.4% of lizards. We specifically identified four of the *Peromyscus* spp. as *P. boylii*, and six of the *Sceloporus* spp. as *S. jarrovii* (Table 1). Seven of the *Cnemidophorus* spp. were obtained from specimens from the Sierra San Luis, and one from the Peloncillo Mountains. All 15 centipedes were identified as *Scolopendra* spp., and only one was found in a sample containing other prey (lizard) remains.

Predator SVL significantly differed among prey classes (Kruskal-Wallis test, $H_{(3)} = 31.8$, $P < 0.001$; Fig. 1). Snakes that consumed birds had greatest SVL ($\bar{x} = 450 \pm 52.2$ mm, N = 5), followed by those that consumed small mammals ($\bar{x} = 422 \pm 64.2$ mm, N = 37), lizards ($\bar{x} = 343 \pm 104.1$ mm, N = 38), and centipedes ($\bar{x} = 268 \pm 61.6$ mm, N = 15). Prey class was independent of mountain range ($G = 8.24$, $df = 6$, $P = 0.221$), sex ($G = 3.35$, $df = 3$, $P = 0.340$), and season ($G = 3.13$, $df = 3$, $P = 0.372$). Figure 2 presents distribution of prey classes among mountain ranges and the sexes.

We captured five species of rodents: *Eutamias dorsalis*, *Neotoma mexicana*, *P. boylii*, *Perognathus flavus*, and *Sigmodon ochrognathus* (Table 2). Composition of trapped small mammals was dependent on habitat ($G = 70.82$, $df = 6$, $P < 0.001$), but did not vary significantly between encinal and talus habitats ($G < 0.01$). Trap success was highest in talus (19.8%), followed by pine-oak (15.8%), encinal (13.8%), and plateau (7.8%). Rodent diversity was highest on the plateau (Table 2). *Peromyscus boylii* comprised 64% of total captures and was most abundant in pine-oak woodland.

DISCUSSION

The diet of *Crotalus willardi* has only been described via scattered anecdotal observations largely restricted to subspecies other than *C. w. obscurus* (Table 3). Most authors postulate that the diet of *C. willardi* consists mainly of lizards (*S. jarrovii*), but note that small mammals, centipedes, and birds are also consumed (Vorhies, 1948; Klauber, 1949, 1972; Manion, 1968; Harris and Simmons, 1975; Armstrong and Murphy, 1979; Lowe et al., 1986). Several authors have suggested that juvenile *C. willardi* rely heavily on lizards, perhaps more so than adult snakes (Klauber, 1949,1972; Ernst, 1992; Greene, 1994). Fowlie (1965) supposed *C. willardi* might feed on *S. jarrovii*, but incorrectly speculated a "…preference for amphibians and frogs, rather than warm blooded prey," based on a presumed affinity for "…quasi-permanent streams." Our data illustrate that while lizards represented large proportions of both juvenile (57.1%) and adult (26.4%) diets, other prey constitute significant portions as well. Noteworthy is the consumption of centipedes (33.3%) by juveniles and of small mammals (62.3%) by adults. Interestingly, adults almost never consumed centipedes, yet only the largest juveniles consumed small mammals. In contrast to reports that *C. willardi* rarely consumes birds, we found that birds represented 9.4% of the adult diet. Although lizards are significant prey throughout life, centipedes and endotherms are clearly important at different life history stages.

Greene (1983) and Arnold (1993) predicted that prey diameter/predator head size, and prey/predator body mass ratios limit smaller snakes to smaller, more elongate prey. Our findings are consistent with this hypothesis: smaller snakes consumed only the smallest and most elongate prey taxa (centipedes, lizards). Why centipedes are essentially absent from the diet of larger snakes is unclear. Given the temporal costs of capture and digestion, ambush-hunting snakes may be under greater selective pressure to maximize prey size. When large prey are abundant, as *P. boylii* is at our Animas site, adult snakes may ignore smaller prey to maximize energetic gains per unit time spent foraging. Greater vulnerability to desiccation and/or predation may result in a more fossorial existence for juveniles, where *Scolopendra* may be more abundant and/or catchable. Conversely, adults may occupy microhabitats where *Scolopendra* are less common, or perhaps, larger snakes have difficulty manipulating small elongate objects using ingestion mechanisms designed to maximize prey size.

Although caudal luring has not been formally reported in *C. willardi*, an observation has been cited as a personal communication by Schuett et al. (1984), Greene (1992), and Strimple (1992). Both *C. w. willardi* and *C. w. obscurus* occasionally have yellow or cream-colored tails at birth (*C. w. willardi*: Martin,

Table 1. Prey consumed by *Crotalus willardi obscurus*. Numbers in parentheses indicate percent of total prey by major taxonomic grouping (Arthropoda, Aves, Mammalia, Squamata).

Prey taxon	Frequency	% total prey	Source
Arthropoda		(15.8)	
Scolopendra spp.	15	15.8	This study
Aves		(5.3)	
Myadestes townsendi	1	1.0	This study (MSB 21341)
Wilsonia pusilla	1	1.0	Marshall, 1957 (UAZ 27943)
Unidentified bird	3	3.2	This study
Mammalia		(38.9)	
Sorex spp.	2	2.1	This study
Perognathus spp.	1	1.0	This study
Peromyscus spp.	24	25.3	This study
Reithrodontomys spp.	1	1.0	This study
Unidentified mammal	9	9.5	This study
Squamata		(40.0)	
Sceloporus spp.	26	27.4	This study
Cnemidophorus spp.	8	8.4	This study
Unidentified lizard	4	4.2	This study
Total	95	100.0	

Table 2. Proportion of small mammals trapped in four high elevation habitats in Animas Mountain, July and August 1996. Parentheses indicate number of individuals captured. Miscellaneous captures include *Eutamias dorsalis* (N = 5), *Perognathus flavus* (N = 2) and *Sigmodon ochrognathus* (N = 1)

Habitat	% *Peromyscus boylii*	% *Neotoma mexicana*	% Miscellaneous
Plateau	19.4 (6)	54.8 (17)	25.8 (8)
Encinal	61.8 (34)	38.2 (21)	0.0 (0)
Talus	62.0 (49)	38.0 (30)	0.0 (0)
Pine-oak	90.5 (57)	9.5 (6)	0.0 (0)
Pooled	64.0 (146)	32.5 (74)	3.5 (8)

1975b, 1975c; *C. w. obscurus*: Holycross, 2000) and neonatal *C. w. obscurus* often have yellowish pigment on the upper and lower labials, rostral, and mental scales (Martin 1976; Holycross, 2000). Most juvenile pitvipers with brightly colored tails use the tail to lure prey (Greene, 1992; Strimple, 1992). An ontogenetic shift in tail coloration and caudal luring behavior is often associated with an ontogenetic shift in diet, from frogs or lizards as juveniles to rodents as adults (Heatwole and Davison, 1976). Thus, ontogenetic shift in tail coloration (and possibly caudal luring behavior) in *C. willardi* may be associated with an ontogenetic shift in diet. However, not all juvenile *C. w. obscurus* possess yellow tails, and those that do lose this pigmentation in their first year prior to the shift in diet reported herein.

Venom ontogeny may parallel changes in diet. Adult *C. w. obscurus* venom (LD_{50} = 6.4 µg/g) was approximately 33% less toxic than juvenile venom (LD_{50} = 4.3 µg/g) using an inbred strain (NSA) of laboratory mice (S. Mackessy, pers. comm.). Preliminary toxicity assays with lizards (*Uta stansburiana*) indicate that juvenile venoms kill lizards significantly faster than adult venoms (S. Mackessy, pers. comm.). Greater toxicity of juvenile venom may result in functional equivalency of the venoms (as observed for *C. viridis*; Mackessy, 1988), due to the significantly smaller quantities of venom produced by juveniles. Additionally, because the range of potential prey is smaller for juvenile than for adult *C. w. obscurus* (due to size constraints), higher toxicity of venom ensures that prey are rapidly immobilized and retained once envenomated. Based on preliminary results with *U. stansburiana* and on diet analysis, we predict that ontogenetic venom toxicity differential will be even greater for lizards than that observed for mice (similar

Table 3. Summary of original prey records for *Crotalus willardi* (exclusive of *C. w. obscurus*). * = prey consumed in captivity.

Prey	Reference
Arthropoda	
Centipede	Fowlie, 1965; USNM 46326 (A. Holycross, unpublished)
Centipedes*	Lowe et al., 1986
Scorpion	A. E. Ball, pers. comm. in Klauber, 1972
Aves	
Wilsonia pusilla	Marshall, 1957
Aimophila ruficeps	Parker and Stotz, 1977
Mammalia	Van Denburgh, 1922; Armstrong and Murphy, 1979; Klauber, 1949, 1972
Laboratory mice*	Kauffeld, 1943; Bogert and Degenhardt, 1961; Martin, 1975b, 1976; Tryon, 1978
Peromyscus spp.	Martin, 1975a
Peromyscus boylii	Woodin, 1953
Thomomys spp.	H. Greene, pers. comm.
Squamata	
Elgaria kingii	Klauber, 1949, 1972; F. Wilson and H. Greene, pers. comm.
Sceloporus jarrovii	Klauber, 1949, 1972; Woodin, 1953
Urosaurus spp.*	Martin, 1975b, 1976
*Anolis carolinensis**	Bogert and Degenhardt, 1961
*Hypsiglena torquata**	Vorhies, 1948
*Trimorphodon biscutatus**	Lowe et al., 1986

to *Bothrops jararaca*; Andrade and Abe, 1999) and further tests are in progress.

Our data illustrate that adult *C. w. obscurus* prey frequently on *Peromyscus* spp. Though only four records were positively identified as *P. boylii*, we expect that most unidentified small mammals and all *Peromyscus* samples are *P. boylii*, for several reasons. Our limited trapping results and surveys by Cook (1986) suggest *P. boylii* is the only *Peromyscus* syntopic with *C. w. obscurus* in the Animas Mountains. Our rodent trapping results indicate that *P. boylii* is the most abundant (trappable) small mammal across habitats (64%), representing 90.5% of captures within pine-oak woodland and 62.0% within talus, the two habitats most heavily utilized by *C. w. obscurus* with radiotransmitters. *Peromyscus boylii* is terrestrial and arboreal (Holbrook, 1979; Cook, 1986) and relies heavily on acorns, juniper fruit, and mistletoe (Jameson, 1952; Smartt, 1978). During radiotracking we regularly observed *C. w. obscurus* in classic hunting postures (*sensu* Reinert et al., 1984) at the base of partially felled trees, and along fallen branches and logs used by *P. boylii* as runways into the canopy or along the ground. An observation of predation on *Peromyscus* spp. in the wild (Martin, 1975a) suggests *C. willardi* prey on small mammals by strike-and-release, followed by strike-induced chemosensory searching (SICS; Chiszar et al., 1977; Stiles et al., this volume).

Similarly, we expect that most *Sceloporus* records from the Animas Mountains are assignable to the syntopic (and abundant) *S. jarrovii*. *Sceloporus virgatus* occurs at lower densities and in more open habitats where *C. w. obscurus* was infrequently encountered, and *S. clarkii* occurs below the lower elevational records for *C. w. obscurus* in this mountain range. In other ranges *C. w. obscurus* occurs at lower elevations and is syntopic with *S. virgatus*, *S. clarkii* and *S. grammicus*. In the Peloncillo Mountains and lower elevations of the Sierra San Luis, where *S. jarrovii* is less abundant, *C. w. obscurus* may rely more on these and other lizard species, as suggested by the eight records of *Cnemidophorus* spp. obtained from these sites. Both *C. exsanguis* and *C. sonorae* are syntopic with *C. w. obscurus* and may be represented among fecal samples referred to this genus. It is unclear whether *C. willardi* strike-and-release or retain (hold) lizards; our limited field observations of congeners in similar ecological settings suggest both strategies may be used. The microhabitats in which *C. willardi* adopt ambush postures for lizards and the postures themselves differ from those used for rodents. Several individuals, particularly juveniles, were observed in loose S-shaped postures during the day, against sides of rocks or in vertical fissures. The head was directed toward the top of the rock. Since this is a preferred habitat for *S. jarrovii*, and *P. boylii* is largely nocturnal, we assume these individuals were ambush hunting for lizards (see Downes and Shine, 1998). Interestingly, although *Elgaria kingii* have been identified from the stomachs of *C. w. silus* and *C. w. willardi* (Table 3), this syntopic and moderately abundant lizard is absent from our sample. *Elgaria kingii* appears to rely heavily on chemosensory stimuli and may avoid rattlesnake odors.

The high number of solitary centipede records, a skewed distribution among snake size classes, and observations in captivity all suggest direct foraging on live centipedes rather than secondary ingestion or incidental scavenging of dead ones. Indeed, the first *C. willardi* collected and later deposited in a museum (USNM 46326; Nelson Goldman Expedition, Colonia Garcia, Chihuahua, 3 July 1899) is a small *C. w. silus* that contains a large, intact *Scolopendra* sp., swallowed headfirst. Large centipedes are not uncommon in the diet of several other rattlesnakes (e.g., *Sistrurus miliarus*, Hamilton and Pollack, 1955; *C. enyo*, Taylor, 2001; *C. lepidus klauberi*, Holycross et al., in press; *S. catenatus edwardsii*, Holycross and Mackessy, 2002). Centipede eaters may have evolved specific adaptations for foraging on venomous prey. Rubio (1998) wondered if centipede eaters are somewhat resistant to centipede venom, and two observations suggest centipede-specific prey handling behaviors. *Crotalus w. willardi* preying on centipedes in captivity raise the anterior half of the body above the prey, strike down and release, and then rapidly retreat (H. McCrystal, pers. comm.). On the other hand, Rubio (1998) described a predatory sequence by a captive *C. lepidus* wherein a centipede was struck just behind the head and was not released prior to ingestion. We were unable to determine direction of ingestion in this study because all of our centipede records were identified from fecal remains. Centipedes found in the stomachs of *S. c. edwardsii* (and USNM 46326 cited above), however, were all swallowed headfirst judging by orientation in the stomach (Holycross and Mackessy, 2002).

A single field observation suggests *C. willardi* strikes and restrains birds using the mouth and body (Parker and Stotz, 1977). Pitvipers rely on SICS to follow the trail of envenomated terrestrial prey, a foraging strategy incompatible with flying prey. It is unclear what cues rattlesnakes use to determine predatory response, but the observation of arboreal foraging on birds (Parker and Stotz, 1977), and our recurrent observations of radiotagged individuals perched in trees and low bushes (see also Rossi and Feldner, 1993), suggest *C. w. obscurus* may adopt foraging postures specifically for birds, perhaps in response to chemical cues on frequently used perches.

Woodlands, adjacent talus slopes, and rock outcrops play a central role in the foraging ecology of *C. w. obscurus*. *Peromyscus boylii* is most abundant in these habitats (Table 2) and adult snakes exhibit foraging tactics that use structural components of woodland. Likewise, talus slopes and rock outcrops near woodlands support the highest densities of *S. jarrovii*. *Scolopendra* spp. are probably more abundant in forest leaf-litter and in talus than on hot, exposed grassy slopes. Identified avian prey species are associated with woodlands and chaparral. At our Animas site, *C. w. obscurus* were infrequently encountered in immediately adjacent open habitats where encounters with humans were much more likely; they also occur in much lower densities in mountain ranges where pine-oak communities are less developed, such as the Peloncillo Mountains. The foraging ecology of *C. w. obscurus* is predominately adapted to woodland and talus communities, which may play a role in habitat selection. Clearing of woodlands, by mechanical means or by stand-replacing, natural or management-ignited catastrophic fire, would undoubtedly negatively affect *C. w. obscurus* prey communities and structural components of habitat used in foraging. Preservation of encinal and pine-oak woodlands and associated faunal communities is essential to the conservation of this federally threatened rattlesnake.

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