

*Crotalus willardi*

## RIDGE-NOSED RATTLESNAKE

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■ **TAXONOMY.** *Crotalus willardi* was named and described by Seth Eugene Meek (1905), who listed the type locality as “Tombstone, Arizona.” Swarth (1921) corresponded with the collector and namesake, Francis C. Willard, who stated that he collected the type specimen (FMNH 902) “a short distance above Hamburg in the middle branch of Ramsey Canyon” in the Huachuca Mountains in the summer of 1900. Willard lived in Tucson from ca. 1896 to 1916 and was an avid ornithologist and naturalist (Moll 2003a).

Five subspecies have been described, two of which occur in AZ: *Crotalus willardi willardi* (Arizona Ridge-nosed Rattlesnake) and *Crotalus willardi obscurus* (New Mexico Ridge-nosed Rattlesnake; Harris and Simmons 1976). The remaining three subspecies are endemic to México: *Crotalus willardi amabilis* (Del Nido Ridge-nosed Rattlesnake; Anderson 1962), *Crotalus willardi meridionalis* (Southern Ridge-nosed Rattlesnake; Klauber 1949b), and *Crotalus willardi silus* (Chihuahua Ridge-nosed Rattlesnake; Klauber 1949b).

The name “*Crotalus willardi obscurus*” was first used (occupied) by Harris (1974) in a popular article in which Harris pled for listing the Animas Mountains (NM) population under the federal Endangered Species Act. However, Harris (1974) did not provide a description, definition, or diagnosis (nor did he reference a published description) when he used the name, instead referring to it as a “manuscript name.” Harris and Simmons (1976) later published a “formal description” in a regional herpetological society publication edited by Harris. Smith *et al.* (1975) used this as an example of homoplasmism but regarded the name *obscurus* as available because, as they wrote, Harris (1974) included “a photograph and brief notice of some characteristics” of the proposed subspecies. Citing Smith *et al.* (1975), McCranie and Wilson (1979) came to the same conclusion;



FIGURE 1. *Crotalus willardi* (Ridge-nosed Rattlesnake) from the Patagonia Mountains, Santa Cruz Co. Photo by Timothy A. Cota.

as evidence of a description, they noted that Harris (1974) included “a photograph of a paratype of the subspecies, as well as an oblique reference to the distinctive characteristics of the taxon.” However, Harris (1974) did not reference type material of any kind, the photograph in question is not captioned, and we cannot find any mention (oblique or otherwise) of any character that could be used to differentiate the proposed taxon from conspecifics, let alone a description. The International Code of Zoological Nomenclature (ICZN 1999) clearly stated that in order to be available, a new name must “be accompanied by a description or definition that states *in words* characters that are purported to differentiate the taxon” (emphasis ours) or include bibliographic reference to a published statement that does the same. As used in Harris (1974), *obscurus* is a model *nomen nudum*. Thus, the name’s establishment is associated with Harris and Simmons (1976), and not Harris (1974) as reported in some publications and synonymies (*e.g.*, Campbell and Lamar 2004; Barker 2016). The holotype (USNM 195546) of *C. w. obscurus* was collected in September 1965 by Charles Hanson in “upper end Indian Creek Canyon, Animas Mountains, Hidalgo County, New Mexico” (Harris and Simmons 1976). The taxonomic practices of Harris (1974) and Harris and Simmons (1976, 1978) were roundly criticized by McCranie and Wilson (1979), and some later authors omitted reference to *C. w. obscurus* (*e.g.*, Armstrong and Murphy 1979). Barker (1992)

subsequently supported subspecific recognition based on an analysis of rangewide variation in morphology and allozymes.

Appealing to the evolutionary species concept, Barker (2016) recommended elevation of all five currently recognized subspecies to full species rank, based in part on (1) his previously published allozyme and morphological data (which did not recommend elevation), (2) a multi-locus study of neutral nuclear loci in one subspecies (Holycross and Douglas 2007), and (3) unpublished molecular sequence data. Significantly, this recommendation was based on neither new published data nor novel analyses of existing data. In the interest of evidence-based taxonomy and taxonomic stability, we await publication of a thorough, multi-locus phylogenetic evaluation of the evolutionary history of the *C. willardi* clade before considering the recognition of multiple species in this clearly monophyletic lineage.

The precise placement of *C. willardi* within the rattlesnake phylogeny has proven most enigmatic. Early attempts based on morphology and venom proteins can be found in Brattstrom (1964) and Foote and MacMahon (1977), respectively. Murphy *et al.* (2002) presented six possible phylogenies based on maximum parsimony analysis of mtDNA sequences. The position of *C. willardi* varied considerably among them; however, their preferred phylogeny placed *C. willardi* as sister to the ancient *triseriatus* clade, which is regarded as the sister clade to all other *Crotalus* spp. (Wüster 2017). A multi-locus phylogenetic study found “weak to moderate support for *C. willardi* as a basally divergent member of the *C. durissus* group” (Reyes-Velasco *et al.* 2013). A phylogenetic analysis of the Crotalinae based on mtDNA sequence data (Castoe and Parkinson 2006) and a multi-locus evaluation of the phylogeny of the Colubroidea (Pyron *et al.* 2011) both placed *C. willardi* as sister to the large and diverse *viridis* clade. A multi-locus phylogenetic study of the Squamata placed *C. willardi* as sister to *C. horridus* (Timber Rattlesnake), which was in turn sister to the *durissus* group (Pyron *et al.* 2013). Most recently, a multi-locus phylogenetic



FIGURE 2. *Crotalus willardi* (Ridge-nosed Rattlesnake) from the Animas Mountains, Hidalgo Co., NM. Photo by Don S. Sias.

analysis restricted to the rattlesnakes found moderate support for placement within the *triseriatus* clade (Blair and Sánchez-Ramírez 2016), whereas a multi-locus phylogenetic analysis of the Viperidae found weak support for an association with the *durissus* clade of rattlesnakes (Alencar *et al.* 2016). The points of concurrence among these molecular studies are that *C. willardi* diverged relatively early in the radiation of rattlesnakes, and that it is an unbranched lineage. Interestingly, Stille’s (1987) cladistic analysis of scale microdermatoglyphics also suggested a deeply nested and unbranched *C. willardi* lineage.

**ETYMOLOGY.** The generic name *Crotalus* (Gr. *krotalon*, a rattle) refers to the rattle. The specific name is a patronym honoring Francis Cottle Willard, who collected the holotype (see Moll 2003a). In the first published use of the name *obscurus*, the author stated that the word “is taken from the Latin and means obscure, shady—a perfect name for such a nondescript member of a species” (Harris 1974). However, Brown (1956) indicated that *obscurus* is Latin for “dark, indistinct.”

■ **DESCRIPTION.** Lithe and relatively small, *C. willardi* adults are typically 400–500 mm SVL. The longest *C. willardi* reported in the literature was a male *C. w. silus* born in captivity that measured 710 mm TL at its death, despite missing the end of the tail (UTA 19413; Barker 2016). The maximum length reported for a wild individual was a male *C.*

*w. obscurus* captured on Indian Peak in the Animas Mountains that measured 668 mm TL (601 mm SVL; Keegan *et al.* 1999). The longest individual from AZ was a captive *C. w. willardi* from the Huachuca Mountains that measured 662 mm TL (UTA 17856; Barker 1992). In their sample of all age classes of *C. w. willardi* from the Huachuca and Patagonia mountains, McCrystal *et al.* (1996) found that males measured 254–492 mm SVL ( $\bar{x} = 375.2 \pm 26.0$ ,  $n = 12$ ), and females measured 234–412 mm SVL ( $\bar{x} = 348.3 \pm 15.7$ ,  $n = 11$ ); males weighed 16–140 g ( $\bar{x} = 63.8 \pm 11.4$ ,  $n = 12$ ), and females weighed 16–88 g ( $\bar{x} = 43.3 \pm 6.1$ ,  $n = 11$ ). Morphometric data associated with samples of

**TABLE 1.** Snout-vent length and mass of adult male (> 406 mm SVL) and adult female (> 402 mm SVL) *Crotalus w. obscurus* (New Mexico Ridge-nosed Rattlesnake) from the Animas Mountains, NM (1993–2016), and the Sierra San Luis, Sonora, México (2003–2018). Study sites in the Sierra San Luis include Cañon San Luis, Rancho Pan Duro, and “Study Canyon” in the northern Sierra San Luis.

Site	SVL in mm ( $\bar{x} \pm SD$ , $n$ )	Mass in g ( $\bar{x} \pm SD$ , $n$ )
Animas ♂	410–601 (485.8 ± 43.1, 93)	56.0–263.0 (122.6 ± 40.7, 94)
Animas ♀	402–549 (455.6 ± 33.2, 89)	52.0–181.0 (97.0 ± 28.5, 89)
Cañon San Luis ♂	406–503 (459.6 ± 35.6, 11)	47.9–145.6 (88.1 ± 29.7, 11)
Cañon San Luis ♀	402–531 (457.1 ± 29.4, 22)	55.6–123.1 (81.4 ± 18.0, 22)
Rancho Pan Duro ♂	406–525 (446.5 ± 30.6, 28)	47.5–137.6 (80.7 ± 19.6, 28)
Rancho Pan Duro ♀	402–506 (428.8 ± 24.1, 39)	41.3–144.3 (69.2 ± 21.0, 39)
“Study Canyon” ♂	436–536 (486.2 ± 29.6, 9)	64.9–154.8 (110.0 ± 27.3, 9)
“Study Canyon” ♀	405–514 (443.2 ± 30.7, 9)	50.3–151.2 (75.3 ± 31.8, 9)

adult *C. w. obscurus* from the Animas Mountains and Sierra San Luis, Sonora, México, are presented in Table 1. Tail length as a percentage of SVL for adults from the Animas Mountains was 7.3–9.8 ( $\bar{x} = 8.3 \pm 0.5$ ,  $n = 86$ ) for females and 9.1–13.4 ( $\bar{x} = 10.6 \pm 0.8$ ,  $n = 85$ ) for males.

Perhaps the most distinctive feature of this species is the upturned ridge along the anterior aspect of the *canthus rostralis*, which is responsible for the common name (Figs. 1 and 2). Compared with other rattlesnakes, *C. willardi* has a proportionately long and relatively narrow head (Figs. 1 and 2; Klauber 1938a), fangs that are long relative to body length but of typical length relative to head length (5.3–6.0 mm,  $n = 5$ ; Klauber 1939c), a relatively long tail, and a proportionately larger rattle (mean depth of the proximal segment is 5.8 mm; Rowe *et al.* 2002). Mean number of segments in the rattle string of 55 museum specimens examined by Rowe *et al.* (2002) was 4.6 (10.9% were rattle-less), whereas snakes examined in the field averaged 4.3 segments (Holycross in Rowe *et al.* 2002). Neonates shed the prebutton with the first ecdysis and sometimes shed the button in the second ecdysis, an unusual trait in rattlesnakes (Setser *et al.* 2011; J. Porter, pers. comm.). The hemipenes are short, bifurcated, and have lobes with approximately 56 basal spines, 16 fringes per lobe, and one or two spines at the intersection of the lobes (Klauber 1972). Dorsal scale microdermatoglyphics were described and illustrated by Stille (1987). Karyotype is undescribed to the best of our knowledge.

**COLORATION AND PATTERN.** *Crotalus w. obscurus* and *C. w. willardi* differ in dorsal coloration and some elements of pattern. *Crotalus w. willardi* ground color is typically rusty or rich orange-brown (Figs. 3–5), whereas *C. w. obscurus* ground color is usually light gray (Figs. 6 and 7), although in some snakes, the gray is suffused in a light brownish-orange. In a captive and several recaptured wild *C. w. obscurus*, we noticed considerable loss of the brownish-orange color as individuals grew. Across all subspecies, the dorsum is crossed by 19–46 light-cream to white



**FIGURE 3.** *Crotalus willardi* (Ridge-nosed Rattlesnake) from the Santa Rita Mountains, Santa Cruz Co. Photo by Richard Legere.

bars 1–2 scale rows wide, bordered by darker pigment. The bars are about nine scale rows apart and do not usually descend laterally onto the sides of the snake. The spaces between the bars appear as roughly quadrangular dorsal blotches, although the ground coloration of these “blotches” descends laterally onto the sides, where it is usually marked by a series of three rows of darker spots covering 1–4 scales (although the side spots are sometimes faint or absent altogether, especially anteriorly). Ground coloration continues onto the dorsum of the head, which is often marked with small dark or black punctations and irregularly shaped flecks. The venter is cream anteriorly, sometimes becoming darker posteriorly and flecked with darker pigment. The subcaudals are similarly colored and marked. The pupil is vertical, irises speckled in black vary from a light-bronze to gray, and the tongue is black, sometimes with gray tips.

In *C. w. willardi*, the sides of the head are boldly striped in white on rich, dark reddish-brown (Fig. 1 and frontispiece to Viperidae). An approximately one-scale-wide, bright white stripe runs diagonally downward from near the tip of the nose, above the facial pit, to approximately the 7th or 8th supralabial, thence following and covering the remaining supralabials to the corner of the mouth, where it connects with the white of the throat. Another white stripe covers the first 5–6 supralabials and then falls diagonally below the mouth to meet the white of the throat. A white medial line on the rostral and mental scales connects to the white of the throat, splitting reddish-brown patches on the undersides of the chin. In *C. w. obscurus*, the sides of the head are gray to brownish-gray, and the striping is absent or considerably reduced (Fig. 2). When present, the upper white stripe is faintly present posterior to the eye. The lower white stripe is muted



FIGURE 4. *Crotalus willardi* (Ridge-nosed Rattlesnake) from the Huachuca Mountains, Cochise Co. Photo by Kenny Sharrocks.

to absent. Some *C. w. obscurus* completely lack stripes on the side of the head. The considerable variability in the position and extent of facial striping in the species as a whole is extensively described and illustrated elsewhere (Campbell and Lamar 2004; Barker 2016).

One to three blotches (sometimes bands) are found on the proximal portion of the tail. *Crotalus willardi* is unique among AZ rattlesnakes in having longitudinal stripes (gray and brown or gray and black) on much of the distal portion of the tail in adults, although this striping is frequently faint and sometimes absent, producing instead a gray to brown, unicolored tail tip. Tail tips of neonates are striped or solid and range from yellow to gray to black in ground color (Fig. 8; neonatal tail coloration is reviewed in Holycross 2000c). Some neonates have yellow pigment on the labials, which fades rapidly with age; otherwise, the labials are patterned as in adults.

**SCUTELLATION.** The internasal and anterior canthal scales flare upward, producing the characteristic upturned ridge along the anterior aspect of the *canthus rostralis* for which the species is named. The remaining scales on the dorsum of the snout (anterior of the supraoculars) are small and numerous (20–40). The supraoculars are separated on the top of the head by 6–9 small scales. The rostral is taller than wide. Laterally on the



FIGURE 5. *Crotalus willardi* (Ridge-nosed Rattlesnake) from the Huachuca Mountains, Cochise Co. Photo by Brandon LaForest.

head are 2 loreals (rarely 1), 12–17 right and left supralabials, and 12–17 right and left infralabials. A single, disproportionately large prenasal and a single postnasal together surround each nare. Snakes from northern localities typically have 25 scale rows at mid-body, although rangewide the number of dorsal scale rows at mid-body is 25–29. Dorsal scale rows are keeled, with the exception of the lowest three rows on the sides, which are smooth. Males have 146–158 ventrals and 25–36 subcaudals. Females have 147–159 ventrals and 21–31 subcaudals. The cloacal scute is entire. The subcaudals are mostly entire, with some divided toward the tip of the tail. The rattle fringe scales are pointed and flare outward at the base of the proximal segment. Meristic data reported above are from Campbell and Lamar (2004). In the Huachuca and Patagonia mountains (*C. w. willardi*), subcaudals numbered 24–30 ( $\bar{x} = 27.7 \pm 0.53, n = 12$ ) for males and 22–27 ( $\bar{x} = 24.4 \pm 0.47, n = 11$ ) for females (McCrystal *et al.* 1996). In the Animas Mountain population (*C. w. obscurus*), subcaudals numbered 25–33 ( $\bar{x} = 29.9 \pm 1.5, n = 66$ ) for males and 20–29 ( $\bar{x} = 24.8 \pm 1.8, n = 71$ ) for females.

**SIMILAR SPECIES.** *Crotalus lepidus* and *Crotalus pricei* are also small, montane rattlesnakes that co-occur with *C. willardi* in some locations. Although either species may be confused with



FIGURE 6. *Crotalus willardi* (Ridge-nosed Rattlesnake) from the Peloncillo Mountains, Hidalgo Co., NM. Photo by Bruce L. Christman.

*C. willardi* by an inexperienced observer, both are readily differentiated by color and pattern. *Crotalus lepidus* has black “bands” (as opposed to pale crossbars) on a grayish background and lacks the canthal ridge. Furthermore, *C. w. willardi* has vivid white and reddish facial markings that distinguish it from *C. lepidus klauberi*. In the Peloncillo Mountains (AZ and NM), both *C. w. obscurus* and *C. l. klauberi* are gray overall and have little to no facial marking, but they can still be readily distinguished based on overall pattern and the presence or absence of the canthal ridge. *Crotalus pricei* has distinctive, paired, dark spots running the length of its dorsum. *Crotalus molossus* attains a much larger size and is green with overtones of gray, brown, or yellow, has dark to black, diamond-shaped blotches (sometimes approaching crossbands), and possesses a distinctive black tail and snout.

**DISTRIBUTION AND ABUNDANCE.** *Crotalus willardi* is distributed from Zacatecas, México, north into southeastern AZ and southwestern NM within the Sierra Madre Occidental and Madrean Archipelago. Within the United States, *C. w. willardi* is known only from AZ and has been found in the Huachuca, Patagonia, Santa Rita, and Whetstone mountains, and in the Canelo Hills (Map 8). Two specimens (UAZ 37757 and 41788) were taken from Campini Mesa, on the southern bajada of



FIGURE 7. *Crotalus willardi* (Ridge-nosed Rattlesnake) from the Animas Mountains, Hidalgo Co., NM. Photo by William R. Radke.

the Huachuca Mountains. Table 2 provides dates of discovery, voucher numbers, and relevant literature associated with the discovery of all populations of *C. willardi* in the United States.

*Crotalus w. obscurus* is restricted to the Animas (NM) and Peloncillo mountains (AZ and NM) in the United States and occurs in the Sierra San Luis in México (Chihuahua and Sonora). Robert Zeller

TABLE 2. Discovery dates of U.S. populations of *Crotalus willardi* (Ridge-nosed Rattlesnake).

Year	Mountain Range	1st Voucher(s)	Relevant Literature
1900	Huachuca Mountains, AZ	FMNH 902	Meek 1905; Swarth 1921
1907	Santa Rita Mountains, AZ	USNM 39896	Hartman 1911
1957	Animas Mountains, NM	AMNH 79056, 81796	Bogert and Degenhardt 1961
1979	Patagonia Mountains, AZ	UAZ 43281	unpublished
1981	Peloncillo Mountains, NM	NMSU 6610, MSB 61232	Campbell <i>et al.</i> 1989
1991	Whetstone Mountains, AZ	UAZ 49176	Thirkhill and Starrett 1992
1993	Canelo Hills, AZ	MVZ 229970	unpublished
1996	Peloncillo Mountains, AZ	AMNH 142597	Holycross and Smith 1997



FIGURE 8. Tails of two neonatal *Crotalus willardi* (Ridge-nosed Rattlesnake) born to a female from the Peloncillo Mountains, Hidalgo Co., NM. Photo by Andrew T. Holycross.

discovered the first *C. w. obscurus* (née *C. w. silus*) in the United States when he captured a pair (AMNH 79056 and 81796) in the Animas Mountains in 1957 (Bogert and Degenhardt 1961). The 1981 discovery of a hybrid *Crotalus lepidus* × *willardi* (NMSU 6610) on the NM side of the AZ–NM state line provided the first evidence of the species' presence in the Peloncillo Mountains (Campbell *et al.* 1989). Six years elapsed before a “pure” *C. w. obscurus* (MSB 61232) was captured in the Peloncillo Mountains, again on the NM side of the state line (Campbell *et al.* 1989). Almost a decade later, Holycross and Smith (1997) reported the first *C. w. obscurus* from AZ (AMNH 142597). On 17 May 2009, Michael Malawy found a rattlesnake that appears to be a natural hybrid between *C. l. klauberi* and *C. w. willardi* in the Santa Rita Mountains, Santa Cruz Co. (Fig. 9 in the *C. lepidus* account).

In México, *C. willardi* has been found from 1,524 m ASL (Villa *et al.* 2007) to 2,846 m ASL (Ishimatsu and Warfel 2014). In AZ, it occurs as low as ca. 1,600 m ASL (Rado and Rowlands 1981). In NM, it has been found as low as 1,520 m ASL in Pine Canyon, Peloncillo Mountains (ASU HP00164; Fedorko *et al.* 2017). In the Sierra San Luis, elevations are from 1,645 m ASL (at Pan Duro) to 2,251 m ASL (in “Study Canyon”).

**QUESTIONABLE LOCALITIES.** Despite persistent rumors and unverified sightings, there are no reliable reports of *C. willardi* from the Chiricahua Mountains. In 1994, one of us (ATH) obtained a

geriatric *C. willardi* (MVZ 229971) from a collector who reported capturing the snake in Rock Creek Canyon approximately 10 years earlier during a herpetological tour of the sky islands. Morphologically, MVZ 229971 is consistent with *C. w. willardi*, but it has an mtDNA haplotype identical to specimens from the Patagonia Mountains (K. Zamudio, pers. comm.). Furthermore, Holycross and Douglas (1997) dedicated 744 person-hours searching specifically for *C. willardi* in the Chiricahua Mountains in Rock Creek Canyon and other rumored localities but found none. Most significantly, *C. willardi* has never been vouchered from the Chiricahua Mountains despite the presence of a permanent, year-round, biological research station in Cave Creek Canyon and regular visitation throughout the range by thousands of naturalists (including many herpetologists) over the past century. Although absence in this case is biogeographically enigmatic, it is unlikely that *C. willardi* naturally occurs in the Chiricahua Mountains. Historical absence does not preclude paleontological presence, although there are no fossils or other evidence suggesting the species ever occupied the Chiricahua Mountains.

Fowle (1965) reported a record from the Empire Mountains but did not reference a specimen. We were unable to find any *C. willardi* vouchers associated with the Empire Mountains, which lacks both Madrean Evergreen Woodland and coniferous forest (Bezy and Cole 2014).

A 1913 malacological expedition reported “one of the rare Price’s rattlers” (*C. pricei*) in a rock slide “six miles from Coronado” on the toll road “from Solomonville to Coronado” (Pilsbry and Ferriss 1918; Ferriss 1919). Coronado was a train station on the south bank of the Gila River, ca. 1.6 km south of Threeway. The snake was “hustled into a Velvet Joe tobacco can” and later “drowned in the Gila.” Although the snake was clearly collected by Ferriss’s party, there is no known specimen supporting the observation. The description places the observation at ca. 1,500 m ASL in the Black Hills at the northern tip of the Peloncillo Mountains in what is now Greenlee Co. However, the elevation is low and does not appear to harbor

appropriate habitat for *C. pricei*, leading Nickerson and Mays (1970) to suggest the specimen may have been a misidentified *Crotalus cerberus*, the juveniles of which are grayish (the nearest *C. cerberus* specimen is from ca. 10 km away on the south side of Turtle Mountain). A misidentified *C. w. obscurus* is another remote possibility. This small, gray form of *C. willardi* was not described until more than six decades after Ferriss’s explorations and would have been unknown to him. *Crotalus w. obscurus* is known from the Peloncillo Mountains, albeit ca. 150 km to the south (along the arc of the range) at 1,520 m ASL in Pine Canyon. However, much of the habitat between Pine Canyon and the Black Hills is exceptionally arid and seemingly unsuitable for *C. w. obscurus*.

**STATUS AND TRENDS.** The Huachuca, Patagonia, and Santa Rita mountains appear to support stable populations of *C. w. willardi* (Johnson and Mills 1982; Johnson 1983). In the Canelo Hills, *C. w. willardi* occurs at lower densities and is supported by four vouchered observations, all from essentially the same locale. The Whetstone Mountains population is known from a single voucher (UAZ 49176; Thirkill and Starrett 1992) and two subsequent field observations (R. Repp, pers. comm.). Turner *et al.* (1999, 2003) invested 253 person-days searching for reptiles in the Whetstone Mountains and found no *C. w. willardi*; suitable habitat in the range is limited to one or two canyons (D. Turner, pers. comm.).

*Crotalus w. obscurus* is listed as threatened under the Endangered Species Act (USFWS 1978). Based on mtDNA and microsatellite DNA, Holycross and Douglas (2007) revealed that the three montane populations of *C. w. obscurus* are historically isolated by vicariance, do not represent a single mtDNA gene pool, and are genetically bottlenecked, with the deepest and sharpest declines in the Peloncillo Mountains population. They concluded that the Peloncillo population is ecologically non-exchangeable with other populations (see also Goode and Parker 2013), warrants recognition as an evolutionarily significant unit and meets legal criteria for recognition as a distinct



FIGURE 9. A juvenile *Crotalus willardi* (Ridge-nosed Rattlesnake) from the Huachuca Mountains, Cochise Co. eating a *Scolopendra polymorpha*. Scolopendromorph centipedes are frequent prey for several small rattlesnakes native to AZ (Holycross *et al.* 2002a,b; Holycross and Mackessy 2002; Mociño-Deloya *et al.* 2015). The orange coloration in the white facial stripes will fade with age. Photo by Randall D. Babb.

population segment under the Endangered Species Act. Davis *et al.* (2015), combined long-term recapture, radio-telemetry, and molecular data with demographic and niche modeling to evaluate the future of the Animas Mountains population of *C. w. obscurus*. Most of the samples and data used by Davis *et al.* (2015) were collected from a single site in a canyon on the north face of Animas Peak. Effective population size was < 39, census size was 151, and predicted time to extinction was 17 ± 2 years. Although wildfire appeared to significantly impact survival, it was less of a factor over time than small-population demographics and corresponding genetic effects. Under a scenario of moderate climate change, Davis *et al.* (2015) predicted that core climate and habitat areas will shift ca. 763 km north to the San Francisco Mountain region by 2080, with a nearly complete loss of suitable climate and habitat within the current distribution. However, it is unlikely the species could track this northward shift, since much of the intervening habitat is currently inhospitable to this species and only likely to become more inhospitable as climate change advances.

The future of the Peloncillo Mountains population of *C. w. obscurus* appears to be even more tenuous than that of the neighboring Animas

Mountains population. Despite intensive field studies and search effort, only *ca.* 30 reliable sightings have been reported from the Peloncillo Mountains, and only three of these were in AZ. Based on long-term mark-recapture studies, Holycross (2001, 2002) estimated that 4.9 person-days of searching were required to capture a single *C. w. obscurus* in the Animas Mountains, and only 1.8 person-days in the Sierra San Luis, México. By comparison, 36.6 person-days were required to perform the same feat in the canyons of the southern Peloncillo Mountains (Holycross 2001, 2002). Subsequent efforts in the same portion of the Peloncillo Mountains expended 39.9 person-days per *C. w. obscurus* captured (Goode and Parker 2013). Most recently, researchers spent 104.0 person-days searching for *C. w. obscurus* in the vicinity of Skeleton Canyon (NM) and captured a single *C. w. obscurus* (Fedorko *et al.* 2017; Holycross and Christman 2018).

To better assess whether extremely low capture rates in the Peloncillo Mountains were due to actual or apparent rarity based on visual encounter surveys, one of us (MG) used drift-fence and funnel-trap arrays deployed in the two canyons in the Peloncillo Mountains where the largest number of snakes were captured by Holycross's field teams. We erected 450 m of fence with 78 total funnel traps, which we checked daily during six-day interspersed intervals from 8 July to 17 September 2004 and June to September 2005. A total of 5,953 trap-days produced only one individual in a trap and one crawling along a drift fence, which translates into a dismal 0.03% trap-success rate.

Clearly, finding *C. w. obscurus* in the Peloncillo Mountains is exceedingly difficult regardless of the method employed. Goode and Parker (2013) tabulated capture-rate data from a variety of studies from throughout the range of *C. w. obscurus* (Table 3). The incredible variation in

**TABLE 3.** Capture rates for *Crotalus willardi obscurus* (New Mexico Ridge-nosed Rattlesnake) within and among the three mountain ranges in which the subspecies occurs. Search efforts did not take place continuously (every year) during the periods indicated.

Mountain Range	Study Site	Period	Person-Days	Snakes	Person-Days/Snake
Sierra San Luis	"Study Canyon"	1986–2004	299	72	4.2
	Pan Duro	2003–18	184	230	0.8
	El Pinito	1998	87	29	3.0
	Cañon San Luis	2003–04	211	95	2.2
	Combined	1986–2018	781	426	1.8
Peloncillos	Geronimo Trail	1997–2005	701	21	33.4
	Skeleton Canyon	2018	104	1	104.0
	Combined	1995–2018	805	22	36.6
Animas	Indian Creek Canyon	1976–2012	*176	30	5.9
	West Fork Canyon	1976–2002	*35	9	3.9
	Combined	1976–2012	1,562	316	4.9

\*Effort quantified separately for both sites only during 2007–08.

relative abundance among and within the three mountain ranges in which the snake occurs leads us to believe that density-dependent factors likely play a large role in the local ecology of this micro-endemic species.

Habitat in the Peloncillo Mountains is naturally fragmented into isolated, wooded canyons (Holycross and Smith 2001). Johnson and Mills (1982) and Johnson (1983) suggested that "any opening of the vegetation and concomitant drying of the canyon bottoms will have a significant negative impact" on *C. willardi*. A century of fire suppression, due to grazing and some active suppression by the U.S. Forest Service, has resulted in elevated fuel loads within pine-oak canyons. As a consequence, both natural and prescribed fires ignited in June, when conditions are extremely dry, have resulted in loss of habitat (Smith *et al.* 2001). Consistent misapplication of prescribed fire is likely to lead to extirpation of already locally rare terrestrial taxa (such as *C. w. obscurus*) that are strongly associated with pine-oak woodland habitat, especially when exacerbated by climate change. On the other hand, inability to restore fire as a natural component of this system will likely result in further accumulation of fuels, increasing the risk of naturally or unintentionally ignited catastrophic fires that may result in vegetation-type conversion to more xeric grasslands or oak-dominated savannah systems. Restoring the natural role of landscape-scale summer fire and preserving oak and pine-oak woodlands are critical to conservation of this subspecies. Smith *et al.* (2001) concluded that "until fuel loads are reduced, summer fire (prescribed or naturally ignited) poses a significant threat to habitat for *C. w. obscurus*." The threat of extirpation due to habitat loss associated with wildfire or misapplication of prescribed fire is probably even higher in the Whetstone Mountains, where *C. w. willardi* habitat is scarcer and perhaps more marginal. Goode and Parker (2013) suggested that *C. willardi* occupying lower-elevation mountain ranges may be especially susceptible to climate change, because the option to move to higher-elevation habitats is not available.

**HABITAT.** *Crotalus willardi* is endemic to the pine-oak woodland assemblage of the Sierra Madre Occidental and the Madrean Archipelago and is "predominantly adapted to montane pine-oak woodlands" (McCranie and Wilson 1987). Throughout its range, *C. willardi* is mostly limited to mature woodland habitats. Although the species may be encountered in oak savannah and chaparral adjacent to mature woodlands, it has not been found on isolated mountains without a recent (Holocene) paleobotanical history of substantial pine-oak woodland development. In AZ and NM, the species is primarily associated with Madrean Evergreen Woodland but ranges up into lower-elevation Rocky Mountain Montane Conifer Forest (McCrystal *et al.* 1996; Holycross 2002a). Well-vegetated, rocky canyon bottoms with ephemeral or intermittent streams and associated slopes appear to support the highest densities of *C. willardi*, although individuals are sometimes found on the periphery of these habitats in open meadows and grasslands (*e.g.*, Campini Mesa, Cochise Co.). They are frequently found in or near piles of woody debris, rock piles, small rockslides, and the periphery of talus fields. In the Animas Mountains, capture rates indicated that they are most abundant on north-facing slopes. Conspicuous trees in their habitats include a wide variety of oaks (*Quercus* spp.), alligator juniper (*Juniperus deppeana*), one-seed juniper (*J. monosperma*), ponderosa pine (*Pinus ponderosa*), Chihuahuan pine (*P. leiophylla*), and Mexican pinyon (*P. cembroides*). They are found in association with a variety of shrubs, including New Mexico locust (*Robinia neomexicana*), manzanita (*Arctostaphylos pungens*), beargrass (*Nolina microcarpa*), skunkbush sumac (*Rhus trilobata*), mountain mahogany (*Cercocarpus montanus*), silktassel (*Garrya wrightii*), and *Ceanothus* sp. Grasses associated with collection localities include *Aristida*, *Bouteloua*, *Muhlenbergia*, and *Sporobolus*. These plant associations are based on our own observations as well as those reported in McCrystal *et al.* (1996). Applegarth *et al.* (1980) searched for and evaluated potential habitat for *C. w. obscurus* on public lands in southwestern

NM, and Holycross and Smith (2001) mapped core woodland habitat for *C. w. obscurus* in the Peloncillo Mountains in AZ and NM.

To examine potential differences in habitat use among populations, Goode and Parker (2013) quantified "mesohabitat" associated with 98 capture sites from throughout the range of *C. w. obscurus*. They evaluated five populations for seven variables (*i.e.*, % bare ground, % rock, % leaf litter, % tree, % shrub, % grass, and % dead vegetation) measured within a 10 m radius circle centered on each snake location. They also measured percent cover of trees (*e.g.*, pine, oak, and juniper), canopy cover measured with a densiometer, and % canopy cover > and < 2 m within 20 m radius circular plots. Their results revealed remarkable among-population variation in habitat use, including statistically significant within- and among-site differences in all seven habitat variables, dominant tree type, and canopy cover. Clearly, *C. w. obscurus* uses a wide variety of habitats in spite of its limited distribution, emphasizing the fact that a one-size-fits-all management strategy is likely to be ineffective, especially given idiosyncratic fire effects resulting from differences in vegetation communities combined with dramatic differences in relative abundance among populations.

■ **DIET AND FORAGING BIOLOGY.** Holycross *et al.* (2002b) quantitatively assessed diet in *C. w. obscurus* using prey remains extracted from 317 encounters with 246 individual snakes in the field and from one museum specimen. Eighty-nine of these encounters (28.1%) yielded 95 identifiable prey items, 88 from feces and 7 from stomach contents. Most prey originated from the Animas Mountains population, although smaller samples from the Peloncillo Mountains and Sierra San Luis were also included. Diet consisted of 40.0% lizards, 38.9% small mammals, 15.8% scolopendromorph centipedes (Fig. 9), and 5.3% birds. *Sceloporus* spp. (spiny lizards) accounted for 68% of lizards, and *Peromyscus boylii* (Brush Mouse) comprised 65% of mammals consumed. *Peromyscus boylii* and *Sceloporus jarrovi* (Yarrow's

Spiny Lizard) were observed most often in pine-oak and talus habitats where *C. w. obscurus* was frequently encountered in the Animas Mountains. Radio-tagged 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*. Centipedes may be consumed most frequently during the monsoon season, as appears to be the case for sympatric populations of *C. lepidus* (Holycross *et al.* 2002a). Predator SVL significantly differed among prey classes; snakes that consumed birds were longest, followed by those that ate small mammals, lizards, and centipedes. Proportions of prey classes did not differ between the sexes or among seasons or mountain ranges. However, snakes at lower-elevation sites were more likely to have eaten *Aspidoscelis* spp. (whiptail lizards), whereas snakes at the higher-elevation sites were more likely to have consumed *Sceloporus* spp. Holycross *et al.* (2002b) classified snakes < 350 mm SVL as juveniles and those ≥ 350 mm SVL as adults. Although Holycross *et al.* (2002b) did not directly present percentages of prey classes consumed by adults *vs.* juveniles, those data are reported here. Adult diet ( $n = 53$ ) consisted of 62.3% small mammals, 26.4% lizards, 9.4% birds, and 1.9% centipedes. Juveniles ( $n = 42$ ) consumed 57.1% lizards, 33.3% scolopendromorph centipedes, 9.5% small mammals, and no birds.

Mociño-Deloya *et al.* (2015) quantitatively examined diet in *C. w. obscurus* using prey remains extracted from 199 encounters with snakes and identified 103 prey. Their results were confined to two sites (Cañon San Luis, Rancho Pan Duro) in the Sierra San Luis in northern Sonora, México. Diet consisted of 54.4% lizards, 21.4% birds, 13.6% scolopendromorph centipedes, and 10.7% small mammals. Like Holycross *et al.* (2002b), these authors classified snakes < 350 mm SVL as juveniles and those ≥ 350 mm SVL as adults for analysis. Adult diet ( $n = 71$ ) consisted of 50.7% lizards, 28.2% birds, 12.7% small mammals, and 8.4% centipedes. Juveniles ( $n = 32$ ) consumed 62.5% lizards, 25.8% centipedes, 6.3% small mammals, and 6.3% birds. Most

of the findings of Mociño-Deloya *et al.* (2015) confirmed conclusions reached in Holycross *et al.* (2002b). Notably, they did not find significant differences between the sexes in the proportion of prey classes consumed, and they found that the proportion of *Aspidoscelis* spp. and *Sceloporus* spp. differed among sites. They provided additional evidence for a strong ontogenetic shift in diet from lizards and centipedes to mammals and birds. However, in contrast to the findings of Holycross *et al.* (2002b), these authors found that the proportion of prey classes consumed at their two Sierra San Luis sites significantly differed for both juveniles and adults. They also found that the proportion of prey classes consumed differed among mountain ranges after including data from Holycross *et al.* (2002b), specifically noting that adult snakes from their field sites consumed a few more centipedes and a much higher proportion of birds. These studies suggest that *C. w. obscurus* is a dietary generalist when contrasted with other montane rattlesnakes (*e.g.*, *C. lepidus* and *C. pricei*) and is capable of considerable plasticity with regard to the proportion of prey classes consumed at different sites.

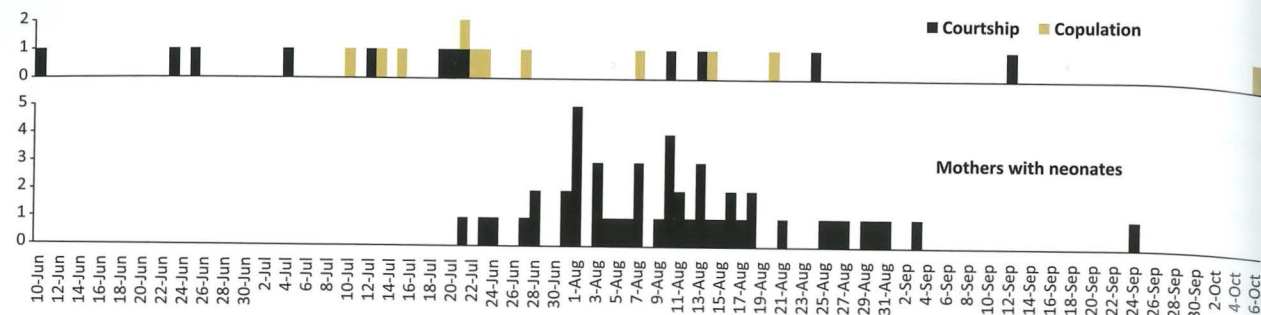
Holycross *et al.* (2002b) also provided a synthesis of *C. willardi* dietary records in the literature, including quantitative data originally reported in Barker (1991) and McCrystal *et al.* (1996). Specific records of prey taken by *C. willardi* in the wild include: *Cardellina pusilla* (Wilson's Warbler; UAZ 27943; Marshall 1957), *Myadestes townsendi* (Townsend's Solitaire), *Aimophila ruficeps* (Rufous-crowned Sparrow; Parker and Stotz 1977), *Sorex* spp. (shrews), *Perognathus* spp. (pocket mice), *P. boylii* (Woodin 1953), *Reithrodontomys* spp. (harvest mice), *Thomomys* spp. (pocket gophers; Bryson and Holycross 2001; Holycross *et al.* 2001; H. Greene, pers. comm.), *Elgaria kingii* (Madrean Alligator Lizard; Klauber 1949b; H. Greene, pers. comm.), *Aspidoscelis* spp., and *Scolopendra* spp. (Klauber 1949b; Fowlie 1965; Greene 1994).

Since this review, predation on *Neotamias dorsalis* (Cliff Chipmunk; Lemos Espinal *et al.* 2007) and *Catharus guttatus* (Hermit Thrush; Mociño

Deloya and Setser 2007a) has been reported in the literature. *Crotalus willardi* may occasionally feed late into the fall or even winter. Setser *et al.* (2005) found a radio-tagged male consuming a *S. jarrovi* on 22 October 1996, a female with a lizard-shaped bolus on 25 October 1996, and a radio-tagged female in a foraging posture on 14 December 2003. From 2007 to 2018, one of us (MG) made a total of seven trips to Rancho Pan Duro in the Sierra San Luis and captured 173 *C. w. obscurus* (113 unique individuals and 60 recaptures), 53 of which contained obvious prey items (based on palpation of anesthetized snakes). With the exception of one individual that contained an unidentified bird, snakes were not forced to regurgitate prey items. One individual was observed consuming a juvenile *S. jarrovi*, another snake consumed a small, unidentified bird, and the feces of one contained centipede chelicerae.

Unidentified bird feathers are protruding from the posterior portion of the holotype (FMNH 902), which is torn nearly in half. On 3 July 1899, the Nelson Goldman Expedition collected the first *C. willardi* specimen (USNM 46326) one year before the specimen that would become the holotype (D. Barker, pers. comm.); it is a young female that contains a large centipede (*Scolopendra*) swallowed headfirst. A captive *C. w. obscurus* kept by one of us (ATH) fed on *Scolopendra* by dramatically elevating the anterior half of its body, striking downward, and rapidly retreating. Both of us have frequently observed *C. willardi* in hunting postures along runways and logs used by rodents, an observation also reported in the literature (Holycross *et al.* 2002b; Setser *et al.* 2005). When preying on birds, *C. willardi* appears to strike and restrain them using its mouth and body (Parker and Stotz 1977). Lists of prey consumed in captivity are provided in several sources (Vorhies 1926b; Manion 1968; Holycross *et al.* 2002b; Barker 2016).

■ **PREDATORS AND PARASITES.** Holycross *et al.* (2001) reported predation by either *Strix occidentalis* (Spotted Owl) or *Buteo jamaicensis* (Red-tailed Hawk) but were unsure of the



**FIGURE 10.** Distribution of observations of courtship ( $n = 11$ ), copulation ( $n = 11$ ), and mothers attending neonates ( $n = 48$ ), by date, for wild *Crotalus willardi* (Ridge-nosed Rattlesnake). Most of these observations were made by John P. Porter from 1983 to 2018 in the Huachuca Mountains, Cochise Co., but observations reported in McCrystal *et al.* (1996), Holycross and Goldberg (2001), and O'Connor *et al.* (2015) are also included.

identification of the predator. Ophiophagous defensive behavior (body bridging) has been recorded in response to *Masticophis taeniatus* (Weldon and Burghardt 1979). Otherwise, predators are unknown but likely include a variety of sympatric raptor species and medium-sized carnivores such as coatis, skunks, and ringtails.

McAllister *et al.* (1996) reported oocysts and sporocysts of *Sarcocystis* sp. (Apicomplexa) from *C. w. obscurus* feces. Goldberg and Bursey (2000a) reported that *C. willardi* is a paratenic (transport) host for larval spiny-headed worms (acanthocephalans) and larval tapeworms (*Mesocestoides* sp.). The bacteria *Salmonella arizonae* and *Providencia rettgeri* have been associated with osteomyelitis and eventual death in captive colonies of *C. willardi* (Ramsay *et al.* 2002).

**BEHAVIOR.** *Crotalus willardi* is active from April or early May through mid-November (Johnson 1983; Lowe *et al.* 1986), although diel activity shifts seasonally. In early spring, snakes are diurnal, shifting to more crepuscular and nocturnal activity as summer approaches. In late May and June, we saw these snakes less frequently aboveground during the height of the day but have observed them in hunting postures in late afternoon and into the night (Kamees 2006). After the onset of summer rains in July, diurnal basking activity increases, particularly by pregnant females. Recent monsoon rains can have a profound effect on capture rates. From 15 June

to 14 July 1995, a crew of four persons searched for *C. w. obscurus* during the day in known habitat in the Animas Mountains and found none. The first monsoon rain of the summer occurred on the afternoon of 14 July 1995, and the crew captured seven *C. w. obscurus* over the next two days. Based on data from 24 *C. w. obscurus* radio-tracked during 1994–97 and in 1999 in the Animas and Peloncillo mountains, both sexes moved more frequently and greater distances during the monsoon season than in spring and early summer (Kamees 2006). Males moved more frequently and greater distances than females in all seasons. By late September and early October, snakes were surface-active more frequently during the day, and radio-tagged individuals were found crawling more often during the day. However, radio-tagged individuals made fewer and shorter movements throughout October and were rarely observed on the surface after mid-November.

Anecdotal observations suggest individuals occasionally overwinter in small groups. On 12 November 1996, two radio-tagged, adult males moved to within 10 cm of each other in a small rockslide, where they remained for the winter. Another adult radio-tagged male was found coiled with a neonate on the same day at a separate, but nearby, location. As mentioned above, a radio-tagged female was found active on 14 December 2003 (Setser *et al.* 2005). In the Sierra San Luis, individuals have been found overwintering 40–46 cm deep in talus slides and surfacing to bask at

air temperatures of 6–9 °C in the shade and 26 °C in the sun (Degenhardt *et al.* 1996). Although *C. willardi* is primarily terrestrial, individuals are occasionally found in the branches of low bushes and trees (Kauffeld 1943a; Parker and Stotz 1977; Rossi and Feldner 1993; Holycross *et al.* 2002b).

In our experience, *C. willardi* is relatively docile and more likely to flee potential predators without rattling than syntopic *C. lepidus*, an observation also noted by McCrystal *et al.* (1996). Mean body temperature of *C. w. willardi* was  $24.2 \pm 0.76$  °C ( $n = 29$ ) in the Huachuca and Patagonia mountains, which was warmer than substrate and air temperatures measured at capture localities (McCrystal *et al.* 1996). Most of the individuals observed at these study sites ( $n = 33$ ) were crawling (39%), basking (24%), or fleeing the observer (15%).

**REPRODUCTION.** Holycross and Goldberg (2001) presented a synthesis of literature records and novel data on reproduction in northern populations of *C. willardi*, which is the basis for the information presented below, unless cited otherwise. The shortest reproductively active individuals measured 406 mm SVL (male) and 402 mm SVL (a pregnant female). Males had enlarged kidney sexual segments and sperm in the *vas deferens* June–October, indicating they are capable of inseminating females during this time. Courtship commenced as early as mid-June, and observations of copulation extended from 13 July (the onset of monsoon) to 6 October, although most records were from late July and August. Although captive females can reproduce annually, several lines of evidence (including data from individual females) indicated that biennial or longer reproductive cycles are the norm in the wild. Females began secondary yolk deposition one or more years following birthing. Ovulation and fertilization appeared to occur early in the spring, followed by 4–5 months of pregnancy. Parturition was observed from 24 July to 30 August ( $n = 15$  litters). Litter sizes were 2–9 ( $\bar{x} = 5.4 \pm 1.6$ ,  $n = 25$ ). Neonates measured 150–182 mm SVL ( $\bar{x} = 167.2 \pm 7.4$ ,  $n = 42$ ) and weighed 5.0–9.0 g ( $\bar{x} = 6.8 \pm 1.2$ ,  $n = 43$ ). Biennial or longer reproductive cycles



**FIGURE 11.** An adult female *Crotalus willardi* (Ridge-nosed Rattlesnake) attending her neonates shortly after parturition in the Huachuca Mountains, Cochise Co., on the morning of 6 August 2014. A total of five neonates were observed with the female and a young adult male visited the site during the period of observation. The female responded to the male's presence with forward and back head jerking, which resulted in the male leaving the area. Photo by Bryan Hughes.

and small litters suggest that *C. willardi* has a relatively low age-specific birth rate and persistence of small populations is likely dependent on adult female survivorship.

Since the publication of Holycross and Goldberg (2001), additional information on the reproductive biology of this species has come to light. Most notable is the large number of observations of dated reproductive behaviors from John Porter's three-decade study of *C. w. willardi* in the Huachuca Mountains, which provide a clearer picture of phenology (Fig. 10). After giving birth, female *C. willardi* spend several days providing parental care to their offspring (Fig. 11; Tanner 1985; Greene *et al.* 2002; O'Connor *et al.* 2015). Males have been observed visiting females with litters and gestating pregnant females (Fig. 11; O'Connor *et al.* 2015), perhaps to determine if the females are receptive to mating. A male *C. w. obscurus* radio-tracked in the Animas Mountains sequentially visited three separate pregnant females over three consecutive days in July. At the Animas Mountains study site, most pregnant females occupied a relatively small area ("maternity slope") with an ESE exposure that was drier and warmer than adjacent areas. In the Sierra Del Nido, Chihuahua, México, a female gave birth to five neonates on 26 July 2000, and

a pair was found copulating (for over 28 hours) on 21 July 2000 (Bryson and Lazcano 2002). In the Sierra San Luis of México, a 453 mm SVL female captured on 8 August gave birth to a litter of five neonates (172–181 mm SVL) on 30 August, one of which was deformed (Mociño Deloya and Setser 2007b). Male combat in this species was documented on 8 August 2008 in the Patagonia Mountains, Santa Cruz Co. (O'Connor and Schuett 2015). Delgadillo Espinoza *et al.* (1999) reported collecting a "gravid female" on 2 May 1993 that gave birth to "two dead embryos and two infertile ova" on 28 July 1993 and later gave birth to five live neonates on 9 August 1993. Reproduction in captivity is described in Martin (1975a,b, 1976a) and Tryon (1978).

■ **REMARKS.** *Crotalus w. obscurus* is listed as threatened under the Endangered Species Act (USFWS 1978). *Crotalus willardi* may reach 23–25 years of age in the wild (J. Porter in Moll 2003a). A captive lived 21 y, 3 mo, and 24 d (Snider and Bowler 1992). If its identity can be confirmed, a fossil from the San Pedro River Valley tentatively identified as *C. willardi* (Mead 1975) might lend credence to the hypothesis that *C. w. obscurus* occupied wooded Pleistocene valleys prior to its current insular distribution (Fowlie 1965). Venom yields and toxicity are low in this species compared to most congeners (Githens and George 1931; Githens and Wolff 1939; Klauber 1972; Minton and Weinstein 1984; Mackessy in Holycross *et al.* 2002b). Saviola *et al.* (2017) examined venom phenotype characteristics, toxicity, and venom variation among and within subspecies of *C. lepidus* and *C. willardi*. They found that *C. lepidus* venom was more toxic to lizard prey and *C. willardi* venom was more toxic to mammals and suggested that these venoms may have evolved to target the primary prey of these taxa (see Holycross *et al.* 2002a,b). Envenomations are rare (but see Minton and Weinstein 1984; Ivanyi and Altamari 2004; Holzman *et al.* 2018). One of us (ATH) was envenomated on the fifth digit of his left hand by a juvenile *C. w. obscurus* while conducting research in the Animas Mountains. He

experienced edema and hypersensitivity to pain throughout his left arm but suffered no lasting debilitation after treatment with Wyeth polyvalent antivenin 12 hours post-envenomation. The only other human envenomations of which we are aware were similarly relatively mild with no lasting disability.

McCrystal *et al.* (1996) provided growth data for six *C. w. willardi*. One male grew from 282 to 433 mm SVL over three years and was found only 11 m from its first capture location. Another male grew from 354 to 401 mm SVL over two years and was 105 m from its first capture location. A female grew from 310 to 380 mm SVL over the course of a year. Barker (2016) provided a history of common names applied to this species in the literature, as well as a list of colloquial names used in México, including names in indigenous languages. Kaufeld's (1957) descriptions of his pursuits of this species in its mountain homes intrigued and inspired a generation of reptile enthusiasts.

■ **ACKNOWLEDGMENTS.** John Porter generously shared data and observations from his three-decade-long study in the Huachuca Mountains. Unless otherwise credited, data and observations from the Animas Mountains and at El Pinito were collected by ATH and colleagues; the Peloncillo Mountains by ATH, MG, and colleagues; Cañon San Luis by K. Setser, E. Mociño-DeLoya, and colleagues; Rancho Pan Duro by MG, K. Setser, and E. Mociño-DeLoya and colleagues; and "Study Canyon" by D. Barker, MG, and colleagues. Our studies have been supported by hundreds of individuals to whom we are indebted. These include colleagues, students, technicians, volunteers, landowners, land and wildlife management agencies, and funding organizations. These persons and organizations are thanked in the acknowledgments of the literature we have published. MG extends special thanks to Ruben Ruiz for supporting his research at Pan Duro and for sharing his unique and entertaining perspective on *la frontera* over the years and ATH extends special thanks to the Animas Foundation for access and assistance over nearly three decades.

## *Sistrurus tergeminus* WESTERN MASSASAUGA

Andrew T. Holycross

■ **TAXONOMY.** *Crotalus tergeminus* was described by Thomas Say (in James 1822) based on two specimens (syntypes) obtained during the Long Expedition to the Rocky Mountains in 1820 by an unnamed collector. James' (1822) account is often cited as appearing in 1823; however, Woodman (2010) recently demonstrated that despite being dated "1823," it was first available for sale on 31 December 1822 in Philadelphia, thus establishing 1822 as the correct year of publication. The syntypes were donated to the "Philadelphia museum" (Charles Willson Peale Museum; James 1822), which was sold to P.T. Barnum in 1848 or 1849, and probably subsequently destroyed in one of the fires that burned Barnum's museum in 1851 and 1865 (Schofield 1989; Stroud 1992; Crother *et al.* 2011). The syntypes have been assigned to a broad array of collection localities (Crother *et al.* 2011), including arbitrary assignments to Winfield, Cowley Co., KS (Smith and Taylor 1950), and the headwaters of the Arkansas River (Schmidt 1953). The International Commission on Zoological Nomenclature (ICZN 2013) designated USNM 86472, collected in 1931 from "5 mi. NW of Winfield," Cowley Co., KS, as the neotype.

Although *C. tergeminus* was described as a species by Say (James 1822), Klauber (1936a) subsumed it within *Sistrurus catenatus*, where it remained until recently. Garman (1884a) erected the genus *Sistrurus* for the southeastern species, *S. miliarius* (Pygmy Rattlesnake). Baird and Girard (1853) described *Crotalophorus edwardsii* (see below for a history of type material), which Cope (1892) synonymized in *S. catenatus*. Klauber (1936a) synonymized *S. c. edwardsii* with *S. c. tergeminus*, although Gloyd (1955) later resurrected it. Thus, for over 50 years, "massasauga" was regarded as a single species, *S. catenatus*, consisting of three subspecies: *S. c. catenatus* (Eastern Massasauga), *S. c.*

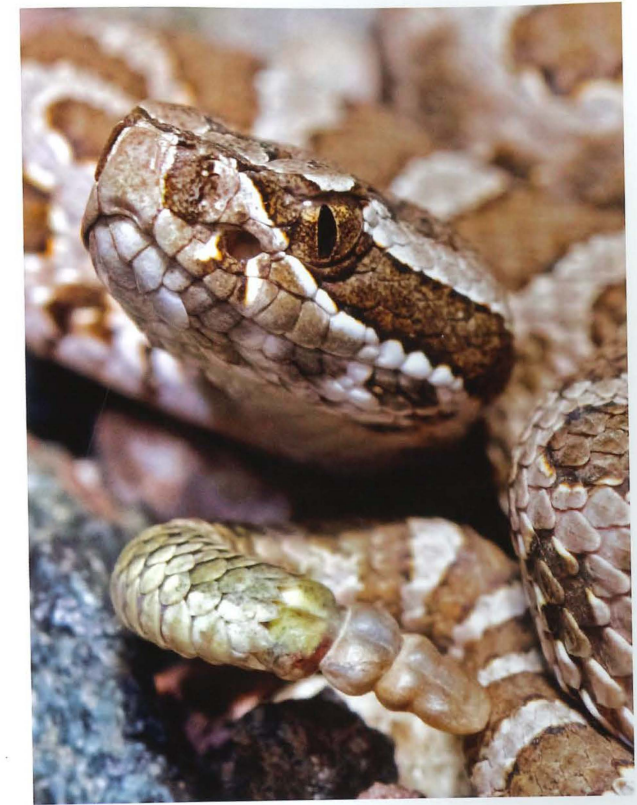


FIGURE 1. *Sistrurus tergeminus* (Western Massasauga) from Ash Flat, Graham Co. Photo by Trent R. Adamson.

*tergeminus* (Western Massasauga), and *S. c. edwardsii* (Desert Massasauga).

Recent phylogenetic studies provide evidence of two highly divergent clades separated by the Mississippi River; an eastern lineage containing *catenatus* and a western lineage comprised of *tergeminus* and *edwardsii* (Kubatko *et al.* 2011; Gibbs *et al.* 2011). Although Kubatko *et al.* (2011) found evidence of genetic distinctiveness in all three putative subspecies, they did not sample extensively west of the Mississippi River, preventing an incisive assessment of phylogenetic patterns in the western clade. They consequently recommended "elevation of *S. c. catenatus* to full species status" under the genealogical species concept, without explicitly recommending taxonomic treatment within the western clade. Their recommendation would have resulted in three new combinations: *S. catenatus*, *S. t. tergeminus*, and *S. t. edwardsii*. However, Holycross *et al.* (2008) had reassigned the type locality of