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 Altimari 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. Kauffeld's (1957) descriptions of his pursuits of this species in its mountain homes intrigued and inspired a generation of reptile enthusiasts.

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

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

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

FIGURE 2. *Sistrurus tergeminus* (Western Massasauga) from the San Bernardino Valley, Cochise Co. Photo by Thomas C. Brennan.

catenatus (Rafinesque 1818) to "the floodplain of the Missouri River, between the mouth of the Platte River and Nebraska City," placing it within the range of *tergeminus* (and the western clade of Kubatko *et al.* 2011). Therefore, the name *Sistrurus catenatus* applied to the western form (rendering *tergeminus* an invalid name), and *massasaugus* (Kirtland 1838), the next available and valid specific epithet, applied to the eastern form (Adler 1963). This nomenclatural problem (anticipated by Gloyd 1940) was resolved by a ruling of the ICZN which retained the names *S. catenatus* and *S. tergeminus* for the eastern and western forms, respectively, and designated a neotype for each (Crother *et al.* 2011, 2012; ICZN 2013).

A subsequent phylogenetic analysis of the western clade (*S. tergeminus*), based on mitochondrial and nuclear genes and extensive geographic sampling, found that "*S. t. tergeminus* and *S. t. edwardsii* populations were genetically indistinguishable" and concluded that they represent polytypic phenotypes rather than subspecies (Ryberg *et al.* 2015). These authors concluded that *S. tergeminus* consists of a historically "large, contiguous collection of populations that only recently became fragmented." Evidence of fragmentation is based on the identification of eight well-supported mtDNA clades comprising three centrally located large clades and five peripheral clades (Ryberg *et al.* 2015).

One of the peripheral clades identified by Ryberg *et al.* (2015) is comprised of specimens from AZ and western NM. Using six microsatellite DNA loci, Anderson *et al.* (2009) found evidence of substantial divergence between populations from the San Bernardino Valley, Cochise Co., and from near Belen, Valencia Co., NM, using multiple measures of genetic differentiation (see also Holycross and Douglas 2001). The findings of Ryberg *et al.* (2015) suggest *S. t. edwardsii* (as traditionally delineated; see Gloyd 1955) is not a monophyletic clade. Nevertheless, the name remains available (nomenclaturally) and is recognized by Crother (2012, 2017). Thus, a history of the type specimens of *S. t. edwardsii* may be of interest to readers of this volume, especially since the sole surviving type material might be from AZ.

Crotalophorus edwardsii was originally described by Baird and Girard (1853) based on three specimens. The holotype (USNM 507) was collected from "Tamaulipas" (México) by a U.S. Army surgeon, Dr. Lewis A. Edwards. The paratypes were collected from "Sonora" (USNM 506) by either Colonel James D. Graham or (more likely) by John H. Clark (Gloyd 1940; Stejneger 1940; Gloyd 1955) and from the "S. Bank of Rio Grande" (USNM 508) by Baird's father-in-law, General Sylvester Churchill (Baird and Girard 1853). The holotype was loaned to Giorgio Jan while he was director of the Museo Civico di Milano, Italy, the herpetological collections of which were destroyed in World War II (Gloyd 1955). One of the paratypes (USNM 508) was missing as of Gloyd's examination of material in the U.S. National Museum in 1932 (Gloyd 1955), leaving USNM 506 from "Sonora" as the sole surviving specimen of the type series. Campbell and Lamar (2004) recounted this history and recognized USNM 506 as the neotype of *S. t. edwardsii*. Although no populations or specimens are known from within the modern political boundaries of Sonora (Bogert and Oliver 1945; Gloyd 1955; Rorabaugh 2008; Rorabaugh and Lemos Espinal 2016), USNM 506 was collected by J.H. Clark and/or Colonel J.D. Graham during the United States–Mexico boundary survey of 1851, when those portions of AZ and NM that lie south of the Gila River were still part of the Mexican state of Sonora. The Graham–Clark expedition apparently travelled through this region on their way from the copper mines east of Silver City, NM to the vicinity of Santa Cruz, Sonora, and back (Graham 1852; Bartlett 1854; Stejneger 1940). This history, interpreted within the context of the extant and historical distribution of this species, indicates that USNM 506 might well have been collected from what is today southeastern AZ (Stejneger 1940; Bogert and Oliver 1945; Gloyd 1955).

The three species in the genus *Sistrurus*—*S. catenatus* (Eastern Massasauga), *S. miliarius* (Pygmy Rattlesnake), and *S. tergeminus*—together comprise a monophyletic group sister to *Crotalus* (Murphy *et al.* 2002; Parkinson *et al.* 2002; Reyes-Velasco *et al.* 2013; Pyron *et al.* 2013; Alencar *et al.* 2016; Blair and Sánchez-Ramírez 2016; Figueroa *et al.* 2016; Wüster 2017).

ETYMOLOGY. The generic name *Sistrurus* (L. *sistrum*, rattle; Gr. *oura*, tail) refers to the rattle, and the specific name *tergeminus* (L. *ter*, thrice; L. *geminus*, twinned or paired) probably refers to the three rows of lateral blotches. The name *edwardsii* is a patronym honoring Dr. Lewis A. Edwards, who collected the type specimen.

■ **DESCRIPTION.** The head is relatively small and narrow for a rattlesnake (Figs. 1–3). Although *S. tergeminus* reaches a maximum of 883 mm TL (Boundy 1995), outlying western populations of the species (*e.g.*, those in AZ, CO, NM, and west TX) are consistently more slender and shorter than populations to the east. The longest *S. tergeminus* collected in AZ measured 541 mm SVL (588 mm TL; ASU 30622; Holycross 2002b). I measured and weighed 65 males and 55 females of all age classes from a population at the northern limits of the San Bernardino Valley, Cochise Co., and report those data here. Males measured 243–541 mm SVL ($\bar{x}$ = 355.8 ± 57.9) and females were 176–523 mm SVL ($\bar{x}$ = 351.2 ± 51.8); however, *ca.* 90% of snakes encountered were 300–400 mm SVL. Males weighed 14.3–112 g ($\bar{x}$ = 38.7 ± 19.9) and females weighed 3.4–94 g ($\bar{x}$ = 35.3 ± 16.4). Tail length was recorded for only a subset of this sample: male tails measured 35–64 mm (n = 30), while female tails measured 27–43 mm (n = 23). Gloyd (1955) reported tail length to total length was 0.104–0.113 ($\bar{x}$ = 0.107) in males and 0.088–0.095 ($\bar{x}$ = 0.092) in females.

In a sample of adult *S. tergeminus* from CO, males measured 259–485 mm SVL ($\bar{x}$ = 355 ± 49, n = 127) and females measured 270–453 mm SVL ($\bar{x}$ = 352 ± 32, n = 87); their mean lengths did not significantly differ (Hobert 1997). Tail length significantly differed between the sexes, with male tails measuring 27–62 mm ($\bar{x}$ = 43 ± 7) and female tails 24–44 mm ($\bar{x}$ = 32 ± 3 mm). In this same population, males weighed 16–116 g ($\bar{x}$ = 42.1 ± 18.6, n = 68) and females weighed 15–60 g (32.8 ± 8.1, n = 67). Hobert *et al.* (2004) also reported mean adult SVL for males ($\bar{x}$ = 355 ± 45 mm, n = 126) and females ($\bar{x}$ = 364 ± 24 mm, n = 69) for the CO population, presumably using much of the same data from Hobert (1997).

Sistrurus and *Crotalus* differ in the shape of the squamosal bone in the skull (Brattstrom *in* Klauber 1972). Dentition includes 1–3 palatine teeth, 7–9 pterygoid teeth, 9–11 dentary teeth, and maxillary fangs (Brattstrom 1964). The fangs of five adult *S. tergeminus* measured 4.5–5.5 mm long, a little longer than average for a rattlesnake of their head length (Klauber 1939c). In *Sistrurus*, each hemipenis is bilobed, deeply forked, and has numerous "robust" basal spines that gradually decrease in size distally until they are replaced by "calyces fringed with spicules" (Gloyd 1940). "This gradual transition from spines to calyces" was regarded by Gloyd (1940) as the chief consistent difference between the hemipenes of *Sistrurus* and *Crotalus*, the latter of which he characterized as having a more abrupt transition. The *sulcus spermaticus* branches once and terminates at the tip of each ramus in a short papilla (Gloyd 1940). McCranie (1988) includes a line drawing of the hemipenis of *S. tergeminus* (UTA 6809). As compared to most species in *Crotalus*, the rattle segments of *S. tergeminus* are small relative to body size. However, as compared to

S. miliarius, the rattle of *S. tergeminus* has larger segments (relative to body size) and the rattle string tends to have more segments (Klauber 1940a; Rowe *et al.* 2002). Rattle strings in the San Bernardino Valley population averaged *ca.* six rattle segments (Holycross *in* Rowe *et al.* 2002).

COLORATION AND PATTERN. A bold, brown eye stripe bordered by thin white margins extends from the eye to behind the corners of the mouth (Fig. 1). Two blotches forming a lyre shape extend from the back of the head onto the neck (Fig. 2). The iris is brown, and the tongue is dark brown with black tips. In AZ, dorsal ground color is often light gray to silver mid-dorsally, becoming suffused with reddish-brown laterally (Fig. 4). Some individuals have darker gray or brownish ground coloration mid-dorsally and are darker overall (Figs. 5 and 6). A single row of roughly elliptical chocolate blotches ornaments the mid-dorsum. Some blotches are pinched mid-dorsally and, in some cases, appear as paired circular blotches ("twin-spotting"). Unlike those found in any other rattlesnake in AZ, these middorsal blotches have smooth, highly contrasted margins that are dark at the edges and often outlined by a thin (sometimes faint) white line.

In a sample of 126 snakes from throughout the distributions of *S. t. edwardsi* and *S. t. tergeminus*, Gloyd (1940) reported 28–45 (x̄ = 38) and 30–50 (x̄ = 40) middorsal blotches for males and females, respectively. Later, in a sample that included only *S. t. edwardsi*, Gloyd (1955) reported 27–41 (x̄ = 35, *n* = 9) and 31–40 (x̄ = 37, *n* = 8) middorsal blotches for males and females, respectively. Laterally, three additional rows of reddish-brown to dark chocolate blotches or spots adorn the sides of the body. The uppermost row of these is the largest and most faded, and blotches in this row are further distinguished by their diffuse borders. Each row of lateral blotches is staggered with respect to the row above. The venter is typically uniformly light gray to light brown with darker flecking. The tail tip is yellowish-orange at birth, but changes within a year to the adult form of light gray with 4–10 brown crossbands. Otherwise, juvenile pattern is the same as in the adult.

SCUTELLATION. Nine large scutes are found on top of the head and include paired internasals, prefrontals, supraoculars, parietals, and a single frontal (Fig. 3). The rostral is taller than wide. Laterally on each side of the head are 7–9 oculars, 1–2 loreals, 10–13 supralabials, and 10–13 infralabials (Fig. 1). Head scalation reported here is based on Gloyd (1940, 1955). Dorsal scale rows at mid-body number 23 in most (>94%) snakes sampled from AZ (*n* = 71) and CO (*n* = 241), but vary from 21 to 25 (Hobert 1997). In a population of *S. tergeminus* from MO (*n* = 34), 88% of specimens had 25 dorsal scale rows at mid-body, but ranged from 23 to 27 (Hobert 1997). All but the lowest two dorsal scale rows are keeled. In a sample of 126 specimens from across much of the range of *S. tergeminus*, Gloyd (1940) reported that males have 140–154 ventrals and 26–34 subcaudals, whereas females have 148–158 ventrals and 21–28 subcaudals. Males from AZ have 137–152 ventrals (x̄ = 143.4 ± 3.1, *n* = 40) and 24–34 subcaudals (x̄ = 30.5 ± 1.9, *n* = 40), whereas females have 140–156 ventrals (x̄ = 147.3 ± 3.4, *n* = 30) and 23–28 subcaudals (x̄ = 25.2 ± 1.3, *n* = 31; Hobert 1997). The cloacal scute and most (but usually not all) subcaudals are undivided. Typically it is the most distal 1–8 subcaudals that are divided.

SIMILAR SPECIES. The presence of the rattle readily distinguishes this snake from similarly patterned colubrids such as *Heterodon kennerlyi*. Among the rattlesnakes, *Crotalus atrox*, *C. cerberus*, *C. molossus*, *C. scutulatus*, and *C. viridis* have been found either syntopically or very near the distribution of *S. tergeminus* in AZ. I have observed one each of *C. cerberus* and *C. molossus* in the grasslands of Ash Flat, Graham Co. *Crotalus atrox* and *C. scutulatus* co-occur with *S. tergeminus* in the San Bernardino Valley. *Crotalus viridis* is not uncommon in the southern San Simon Valley on the NM side of the state line north of Rodeo, NM. Of these rattlesnakes, only juvenile *C. cerberus*, *C. scutulatus*, and *C. viridis* are remotely similar in appearance. Careful examination of color and pattern, as well as the nine large scutes on the top of the head (Figs. 2 and 3), readily discriminate *S. tergeminus* from these species, although *C. scutulatus* has large interoculars (Fig. 9 in the *Crotalus scutulatus* account).

DISTRIBUTION AND ABUNDANCE. In the United States, *S. tergeminus* occurs in relatively isolated populations distributed from western IA, central MO (Evans and Gloyd 1948; Gibbs *et al.* 2011), KS, central OK, central TX to southeastern CO, and southeastern AZ (Gloyd 1955; Kubatko *et al.* 2011). Isolated populations are reported from México at Cuatro Ciénegas, Coahuila (McCoy and Minckley 1969), and near Aramberri, Nuevo León (Minckley and Rinne 1972). The species might occur in northeastern Sonora (Bogert and Oliver 1945; Rorabaugh and Lemos Espinal 2016) and might once have occurred somewhere in Tamaulipas (Baird and Girard 1853; Campbell and Lamar 2004).

In AZ, *S. tergeminus* has been vouchered from the San Bernardino, San Pedro (aka San Rafael del Valle), San Simon, and Sulphur Springs valleys in Cochise Co., as well as from Ash Flat, Graham Co. *Sistrurus tergeminus* appears to have once occurred throughout much of the contiguous San Simon and San Bernardino valleys. A specimen collected by D.B. Carver in 1944 from "21 mi. e. Safford" (CA 12996; Gloyd 1955) documents a historical population at the northern limit of the San Simon Valley, although its precise placement is problematic (see "Questionable Localities"). Interestingly, I found CA 12996 alone in a separately labelled bottle in the Chicago Academy of Sciences (Peggy Notebaert Nature Museum) collection, perhaps a testament to Howard K. Gloyd's perception of its biogeographic importance. Two specimens, one from either side of the AZ–NM state line, provide evidence that a population persisted in the San Simon Valley just southwest of Rodeo, NM, as recently as 1981 (AMNH 107537, MSB 41681; Holycross and Rubio 2000). Over 90% of AZ voucher specimens (*n* = 100) are from a tobosa (*Hilaria mutica*) grassland straddling the divide between the San Simon and San Bernardino watersheds (most of these are DOR specimens collected during my studies of this population and are deposited at ASU). Farther south, several specimens have been collected from the vicinity of Poverty Flats, Cochise Co. (ROM 18224–26, UAZ 39619). The species' historical presence at the extreme southern end of the Sulphur Springs Valley is supported by two specimens from the 1950s (AMNH 81799, UAZ 47272) and two from the 1980s (MVZ 209128, UAZ 48036; Sinclair and Snell 1990).

A specimen (USNM 17789) collected by Dr. Timothy E. Wilcox was deposited in the U.S. National Museum along with a variety of specimens (USNM 17779–98) collected from Fort Huachuca. Wilcox served as post surgeon from 1892 to 1894. More explicit locality information was added (under the same hand, but in a different pen) to the USNM ledger beside the entries for several of these specimens (R. Reynolds, pers. comm.). The locality entry for USNM 17789 indicates its collection from Fort Huachuca (with ditto marks from the record above) and includes the added information, "Parade Grounds, 5200 ft." Although it is not uncommon to find a shipping locality recorded as a collection locality for specimens from this era, the specificity of the data associated with several specimens in this series suggests that they were collected in the immediate vicinity of the fort. The

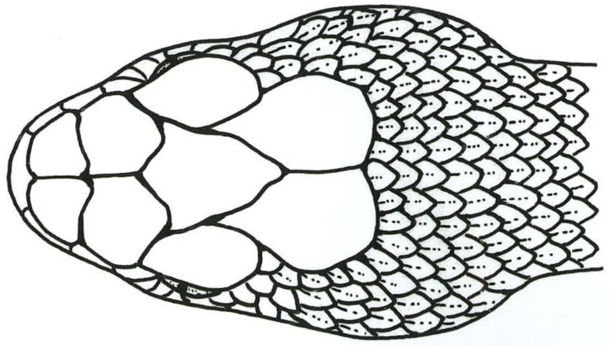

FIGURE 3. *Sistrurus* have nine large scutes on the dorsum of the head (paired internasals, prefrontals, supraoculars, parietals, and a single frontal), whereas *Crotalus* have a single pair of large supraoculars, but otherwise the dorsum of the head is covered with smaller scales (*e.g.*, Fig. 9 in the *Crotalus scutulatus* account). Illustration by Randall D. Babb.

FIGURE 4. *Sistrurus tergeminus* (Western Massasauga) from the San Bernardino Valley, Cochise Co. Photo by Randall D. Babb.

parade grounds reside today precisely where they did in the 1890s, near the mouth of Huachuca Canyon (J. Finley, pers. comm.), which is actually at an elevation of *ca.* 1,550 m ASL. Photographs of the parade grounds from the 1890s portray an open, rocky, and very gently sloping bajada covered with bunchgrass. Stejneger (1902) and Gloyd (1940, 1955) accepted the provenance of the specimen. Unvouchered sightings from near Palominas, Fairbank School, and Hereford (all three in Cochise Co.) in the 1970s and early 1980s (see "Questionable Localities") suggest a population occupying the lowlands of this general region might have persisted until recent times.

One of the most significant recent discoveries in the herpetological biogeography of AZ is the report of a robust population of *S. tergeminus* from Ash Flat in Graham Co. on the San Carlos Indian Reservation (UAZ 57630-PSV; Beauchamp and Calvert 2015). Prior to reporting their find, Jim Beauchamp and Ben Calvert quietly recorded *ca.* 8–9 *S. tergeminus* from Ash Flat from 2001 to 2015 (J. Beauchamp, pers. comm.). Since then, additional photographic vouchers have documented the species across all of Ash Flat (ASU HP00087, 88, and 90). I have observed this species at 1,578 m ASL on Ash Flat (ASU HP00088), which is the highest elevation recorded for it in AZ. The elevation of the Fort Huachuca Parade Grounds where USNM 17789 was collected is slightly lower, at *ca.* 1,550 m ASL. At its reported elevation of 1,006 m ASL, CA 12996 is the lowest specimen documented in AZ.

QUESTIONABLE LOCALITIES. Collectively, the following observations suggest *S. tergeminus* might occur (or have occurred) farther north in Sulphur Springs Valley. There are unvouchered sightings in the mid-1990s on U.S. Highway 191 between Sunizona and Chiricahua National Monument (W. Richardson, pers. comm.). An unvouchered sighting from "2 mi. W of Willcox" in 1968 by "a reliable observer" (T.B. Johnson, pers. comm.) and a sighting from the old Willcox dump (C.J. May *in* Rosen *et al.* 1996b) likely refer to the same observation.

There are also rumored sightings from the 1970s and early 1980s in several places in the San Pedro River watershed, south of I-10. Terry B. Johnson (pers. comm.) conveyed that "Fairbank School, in nearby Sierra Vista, has been spoken of by Lowe as a reputed historic locality for *Sistrurus*." Another sighting is of an uncollected DOR from "7 mi. W of Palominas, Cochise County" seen by another "reliable observer" (T.B. Johnson and J. Jarchow, pers. comm.).

Conflicting information associated with CA 12996 renders it difficult to determine the specimen's precise collection locality. Gloyd (1955) and the museum data associate it with "21 mi. e. Safford," but it is also associated with a collection elevation of "3300 ft" (1,006 m) ASL. When travelling east from Safford by road, whether by modern U.S. Highway 191 (old State Route 71) or U.S. Highway 70 (old U.S. Route 180), elevation gradually increases as one approaches the Peloncillo Mountains. Although these two roadways have undergone some name changes, they remain the only paved roads east out of Safford and follow essentially the same paths they did in 1944 (with minor deviations). In either case, at "21 mi." from Safford, the habitat is atypical and in the foothills of the Peloncillo Mountains (at 1,280 m ASL on U.S. Highway 191 and 1,219 m ASL on U.S. Highway 70). The 1,006 m ASL contour transects both roadways about 21 km (13 miles) east of Safford. I plotted CA 12996 at this location on U.S. Highway 191 on Map 9, where there appears to be suitable habitat.

A specimen (USNM 8409; in four pieces) collected in "Southern Arizona" by Henry W. Henshaw, a naturalist with the Wheeler Expedition, is associated with a collection date of 1874 (and the field number 1307) in the catalog of the U.S. National Museum. Yarrow (1875) associated this specimen with a collection date of "Sept., 1873." Although Henshaw's locations and precise routes of travel during this period are somewhat ambiguous, it appears that he was in the vicinity of Camp Crittenden (4.5 km WSW of Sonoita) during 1–5 September 1874, in the vicinity of Camp (Fort) Lowell (within the modern boundaries of Tucson) during 6–15 September 1874, and in the vicinity of Camp (Fort) Grant during 18–29 September 1874 (Webb and Axtell 1986). Regardless, all of Henshaw's known locations and routes of travel in southern AZ during 1873 and 1874 are peripheral to the historical and extant vouchered distribution of *S. tergeminus*. While other interpretations are certainly possible, it seems likely that USNM 8409 was collected on the Sonoita Plain, in the vicinity of Cienega Creek, or in the northern Sulphur Springs Valley. If the month of collection recorded in Yarrow (1875) is in error (which is not unlikely; see Brown 1966), other localities become possible. For example, Henshaw's travel routes in both 1873 and 1874 crossed Ash Flat, where this species is relatively abundant at present. Due to its imprecise locality information, USNM 8409 is not plotted on Map 9.

There is a slight chance that USNM 19299, collected in 1892 by Edgar A. Mearns (or associates) during the international boundary surveys, was collected in AZ (Gloyd 1955).

STATUS AND TRENDS. This is one of the rarest and most imperiled rattlesnake species in AZ. Across its extensive range in the western United States, relatively few and increasingly shrinking populations of *S. tergeminus* are threatened by climate change, habitat conversion, road mortality, and deliberate extermination. Remaining southwestern populations might be particularly vulnerable to even minor climate change (Greene 1990, 1994). Within AZ, anthropogenic desertification and conversion of grasslands to agricultural fields have resulted in dramatic reduction of an already limited distribution.

The complete lack of recent vouchers from the southern San Pedro watershed (which is transected by numerous roads and has a relatively dense human population) suggests the species is either extirpated or present at extremely low density in this region. Specimens and sightings suggest *S. tergeminus* might yet occupy deteriorated tobosa grassland in the southern Sulphur Springs Valley, although it has been over a quarter of a century since the last voucher was collected. Furthermore, Rosen *et al.* (1996b) logged *ca.* 13,000 km driving road transects throughout the Sulphur Springs Valley from 1993 to 1995 and found no *S. tergeminus*, despite encountering 16 other species of snakes. If *S. tergeminus* remains

FIGURE 5. *Sistrurus tergeminus* (Western Massasauga) from the San Bernardino Valley, Cochise Co. Photo by Randall D. Babb.

in the Sulphur Springs Valley, it is either not abundant, very localized, or both.

Conversion of desert grassland to desertscrub (Hastings and Turner 1965; Turner and Hastings 2003) and a lack of recent vouchers suggest *S. tergeminus* distribution in the San Bernardino and San Simon valleys has substantially receded. The northern end of the San Simon Valley in Graham Co. supported tobosa grasslands and *S. tergeminus* in 1944 (CA 12996), but has since been largely converted to desertscrub and, although I know of one rumor of a recent sighting, no additional vouchers have been produced.

Recent specimens from the San Bernardino and San Simon valleys are restricted to a relict tobosa grassland (*ca.* 1,400 m ASL) straddling the divide between them. In this small and isolated habitat, *S. tergeminus* appeared to have been relatively abundant in the 1990s. Holycross and Douglas (1996) reported that it represented 16.3% of all snakes (*n* = 667) encountered from 1993 to 1995 on a section of U.S. Highway 80 that transects the grassland; only *C. atrox*, *C. scutulatus*, and *P. catenifer* were encountered more frequently. Even so, 47.5% of *S. tergeminus* were found DOR, suggesting that the road may be a significant source of attrition for this population (Holycross and Douglas 1996; Holycross 2003). Despite the presumed reduction in size and geographic range of this population, Anderson *et al.* (2009) found high levels of genetic diversity at microsatellite loci in samples collected in the 1990s (see also Holycross and Douglas 2001). Differentiation among bajadas was weak, and all samples from this population belong to the same "deme," or genetic neighborhood (Anderson *et al.* 2009). Removal of mesquite by local ranchers has abated invasion of desertscrub (R. Krentz, pers. comm.) and might be partially responsible for persistence of the species in this grassland. Anecdotal evidence suggests that *S. tergeminus* is less frequently encountered in this section of roadway than it was in the 1990s and may be declining.

Ash Flat probably hosts the most robust population of *S. tergeminus* in AZ, if catch per unit effort of road-riding is correlated with density. On three separate nights of road-riding, I observed one, four, and seven individual *S. tergeminus*; conversations with other herpetologists suggest that these relatively high encounter rates are not anomalous. The paved road bisecting Ash Flat typically experiences very little traffic (but does infrequently experience heavy traffic), so road mortality is probably much lower than for the San Bernardino population that straddles U.S. Highway 80. Ash Flat is on the San Carlos Apache Indian Reservation where collecting this species is prohibited. Ash Flat is grazed but supports a relatively healthy grassland. Interestingly, *C. scutulatus* appears to be absent from Ash Flat, whereas it is one of the most abundant snakes in the habitat occupied by the San Bernardino population of *S. tergeminus*.

Thus, only two populations of the species are demonstrably extant in AZ; one straddling the San Bernardino–San Simon valley divide and the other on Ash Flat. Conserving these populations will require proactive preservation and restoration of native grasslands. Diversionary structures along portions of U.S. Highway 80 where it bisects the San Bernardino–San Simon Valley population would substantially reduce mortality (Holycross and Douglas 1996).

■ HABITAT. Throughout its range, *S. tergeminus* occupies a broad array of habitat types. In the central and eastern portions of its range, *S. tergeminus* is found in mesic grasslands, wet meadows, and occasionally marshes. In isolated western populations, *S. tergeminus* occurs in short-grass prairies, desert grasslands, grassy dunes, and shinnery oak (*Quercus havardii*) shrublands (Degenhardt *et al.* 1996; Hobert *et al.* 2004; Wastell and Mackessy 2011, 2016). In AZ, *S. tergeminus* has been found only in Semidesert Grassland (Holycross and Douglas 1996; Holycross 2003). The San Bernardino–San Simon Valley population inhabits a tobosa grassland that blankets a volcanic cinder field. *Sistrurus tergeminus* is most often encountered crossing U.S. Highway 80 where it transects the bajadas that gently slope from the base of large cinder cones and less frequently on flats between bajadas (Holycross 2002a; Anderson *et al.* 2009). On these bajadas, loose igneous rocks and wiry bunch grasses are scattered on a surface of friable, red volcanic soils. During the dry spring and early summer, radio-tracked adults often spent their days in the burrows of small rodents. During the late summer rainy season, I often found *S. tergeminus* nestled deep in the base of tobosa clumps, sometimes near *Dipodomys spectabilis* (Banner-tailed Kangaroo Rat) mounds, although the snakes were only rarely found inside the burrows of these large rodents (these burrows are used as refuges by a variety of other reptiles). In December, I found two radio-tracked individuals high on a cinder cone bajada in small rodent burrows with entrances *ca.* 2 cm in diameter.

In an analysis of niche divergence among all putative subspecies of the genus *Sistrurus*, Wooten and Gibbs (2011) found strong evidence for ecological distinctiveness, even between "recently evolved subspecies with minimal genetic differentiation" (referring to *S. t. tergeminus* and *S. t. edwardsii*). They suggested that niche divergence plays a critical role in lineage diversification, particularly in *S. tergeminus*. Temperature and precipitation variables were most important in explaining ecological differences between lineages.

FIGURE 6. *Sistrurus tergeminus* (Western Massasauga) from the San Bernardino Valley, Cochise Co. Photo by Brendan O'Connor.

■ DIET AND FORAGING BIOLOGY. Holycross and Mackessy (2002) conducted a rangewide review of the diet of both *S. catenatus* and *S. tergeminus* using data from their own field and museum work, as well as the published and unpublished literature. The diets of populations of *S. catenatus* from MI and WI and *S. tergeminus* from MO and TX contained more mammals and fewer squamates when compared to the diets of populations of *S. tergeminus* from AZ, CO, and NM. Subsequent to the dietary survey conducted by Holycross and Mackessy (2002), Patten (2006) found that *S. tergeminus* from a NE population consumed 14 small mammals, four snakes (three identified as *Diadophis punctatus*, *Storeria dekayi* [Dekay's Brownsnake], and *Tropidoclonion lineatum* [Lined Snake]), one lizard (*Eumeces septentrionalis* [Northern Prairie Skink]) and one bird (*Spiza americana* [Dickcissel]). Most of the squamates were consumed by juvenile snakes. Diet in the NE population appears to fit the pattern of MO and TX populations of *S. tergeminus* described by Holycross and Mackessy (2002).

Holycross and Mackessy (2002) identified 165 prey from populations of *S. tergeminus* in AZ, CO, and NM, including remains of 97 lizards (59%), 51 mammals (31%), 15 scolopendromorph centipedes (9%), one toad (<1%, *Spea bombifrons* [Plains Spadefoot]), and one snake (<1%, *Tantilla nigriceps*). Diet was surprisingly homogeneous among these three widely separated populations of *S. tergeminus*. Among Cochise Co. samples, *ca.* 76% of prey were abundant diurnal lizards, including *Aspidoscelis uniparens* (33%; Desert Grassland Whiptail), *Sceloporus cowlesi* (28%; Southwestern Fence Lizard), *Holbrookia elegans* (14%; Elegant Earless Lizard), and *Urosaurus ornatus* (2%; Ornate Tree Lizard). Most of the *S. cowlesi* consumed were gravid females. The stomach of one road-killed adult male contained one each of *A. uniparens*, *H. elegans*, and *S. cowlesi*. These lizards were often observed in disturbed areas of open soil, including around *D. spectabilis* mounds. Small mammals represented 24% of diet and included two records of *Notiosorex* (desert shrews) referable to either *N. cockrumi* (Cockrum's Desert Shrew) or *N. crawfordi* (Crawford's Gray Shrew; see Baker *et al.* 2003). Large centipedes were also regularly consumed. Centipedes and mammals appeared to be consumed more frequently during the monsoon season. Holycross and Mackessy (2002) found that *S. tergeminus* from AZ, CO, and NM that were under 250 mm SVL contained only lizard prey. A *Uta stansburiana* (Common Side-blotched Lizard) was palpated from the stomach of a snake from Valencia Co., NM (B.L. Christman, pers. comm.). Greene and Oliver (1965) reported snakes scavenging *Heterodon nasicus* (Plains Hog-nosed Snake) in Wilbarger Co., TX. Fowlie (1965) reported that AZ specimens feed primarily on anurans based on "examination of stomach contents," although neither specific data nor references to specimens were provided.

Juvenile *S. tergeminus* have yellowish-orange tails that they use to lure prey. Reiserer (2002) demonstrated that captive *S. tergeminus* from KS caudal lure for frogs (as do *S. catenatus*; Schuett *et al.* 1984) but do not appear to lure for lizards. Conversely, *S. tergeminus* from AZ lured for lizards but not frogs and "showed no interest in eating frogs" (Reiserer 2002). The primary visual stimulus control appears to be prey movement patterns, as opposed to prey shape (Reiserer 2002). Naïve *S. tergeminus* from AZ did not respond to neonatal mouse visual cues but did learn to recognize these visual cues in behavioral trials. Olfactory cues appeared to be most important in identifying mammalian prey (Reiserer 2002). For example, 18 naïve captive-born *S. tergeminus* killed and ate one-week-old domestic mice without hesitation (B.L. Starrett, pers. comm.).

Sanz *et al.* (2006) used venom proteomes of *Sistrurus* with divergent diets to describe the unique venom composition of closely related taxa and suggested adaptive diversification via natural selection as a causal mechanism. Venom diversity was highest in the taxa that feed primarily on mammals (*S. catenatus* and *S. tergeminus* from KS) and lowest in those that feed primarily on non-mammalian prey (*S. miliarius barbouri* [Dusky Pygmy Rattlesnake] and *S. tergeminus* from CO). Gibbs and Mackessy (2009) described variability in the toxicity of venoms from different *Sistrurus* rattlesnakes with respect to three classes of prey (mice, lizards, and frogs). *Sistrurus catenatus*, *S. tergeminus* from CO, and *S. tergeminus* from KS exhibited uniformly low toxicity to frogs and much higher toxicity to lizards and mammals. They hypothesized that an overall increase in the diversity of venom proteins in the clade containing *S. catenatus* and *S. tergeminus* (as compared to *S. miliarius*) "might be due to selection for additional venom proteins" that allow them "to 'add' mammals to their diets through evolutionary time." *Sistrurus tergeminus* from CO exhibited the highest toxicity to lizards and lacked P-I metalloproteases and a molecule of phospholipase A2 present in all other forms of *Sistrurus* examined. Pahari *et al.* (2007) described the venom gland transcriptome of *S. tergeminus* from CO and detected unique transcripts that encode for three-finger toxins (known primarily in Elapidae) and a novel toxin resulting from transcriptional splicing of two genes.

■ **PREDATORS AND PARASITES.** Two radio-tagged snakes in CO were inferred to have been preyed upon by *Mustela frenata* (Long-tailed Weasel; Wastell and Mackessy 2011). In NM, a *Lanius ludovicianus* (Loggerhead Shrike) was observed carrying a dead *S. tergeminus* (410 mm SVL) that had injuries to its head and neck (Chapman and Casto 1972). Predation by *Buteo swainsoni* (Swainson's Hawk) and *Circus cyaneus* (Northern Harrier) have been reported from CO (Wastell and Mackessy 2016). All three of these avian predators are syntopic with AZ populations. Minton (2001) mentioned a specimen of *Coluber constrictor* "preserved in the act of swallowing an adult [eastern] massasauga." Carpenter and Gillingham (1975) described defenses against attack by kingsnakes.

Goldberg *et al.* (2001) reported the ascarid nematode (*Hexametra boddaertii*) in the stomach musculature of specimens from Chaves Co., NM. They also described larval physalopterid (*Physaloptera* spp.) and encysted larval spirocercid (*Physocephalus* spp.) nematodes among the gut contents of *S. tergeminus*, which they interpreted as dietary byproducts (originating from lizard prey) and not parasites (Goldberg *et al.* 2001).

■ **BEHAVIOR.** In my experience, snakes from the western portion of the range of *S. tergeminus* are unusually alert rattlesnakes that often flee potential predators rather than standing their ground. Compared with other rattlesnakes, these agile snakes also appear to be more predisposed to turn and bite when handled or restrained. They proficiently sidewind in loose substrates (Lowe *et al.* 1986), which may account for presumed sightings of "sidewinders" by eastern Cochise Co. ranchers (Wright and Wright 1957; R. Krentz, pers. comm.). They are active in AZ from April through October, but my observations suggest increased surface activity and movements are associated with spring egress and the advent of monsoon rains. I found that AZ *S. tergeminus* are primarily nocturnal during the summer and most often found moving during the hours following dusk. However, they may be discovered abroad for several hours after sunrise, throughout the night, and in the afternoon on overcast days. In summer, during the day, I often found radio-tagged snakes coiled at or in the base of tobosa clumps or in the mouths of burrows of small mammals (Holycross 2003), although these individuals did not appear to be in hunting postures. Similarly, *S. tergeminus* in CO were primarily diurnal in April and from late September to October, but were mostly active after sunset May–August (Hobert *et al.* 2004).

Wastell and Mackessy (2011) radio-tagged 36 *S. tergeminus* in southeastern CO; 12 of these were monitored for a full active season and included in movement and home range analyses. Across the entire season, snakes moved 0–493 m/day ($\bar{x}$ = 32.3), and the sexes (females were of mixed reproductive states) did not significantly differ in mean distance moved per day. Upon emergence in spring (April), rattlesnakes made directed movements of 1.0–3.5 km ($\bar{x}$ = 1.9 km) from hibernacula in compacted clay short-grass prairie to summer foraging areas in sand hills with mixed grass and sand sagebrush (*Artemisia filifolia*); the sexes did not significantly differ in total migratory distance. During the spring and fall migration periods, individual snakes moved a mean distance of 89.7 m/day. During summer, movements were shorter ($\bar{x}$ = 15.3 m) and non-directional. The total distance moved across the entire active season varied from 3,156.8 to 7,112.3 m ($\bar{x}$ = 4527 m). Although males and females did not significantly differ in total distance moved over the active season, pregnant females moved less than males during the three weeks preceding parturition. Males occupied significantly larger activity areas and core areas than females. Activity areas (95% kernel density) and core areas (50% kernel density) for males and females averaged 103.77 ha and 23.72 ha, respectively. Snakes returned to hibernacula in October. In CO, Wastell and Mackessy (2011) suggested that vernal and autumnal migrations are driven by the non-overlapping distributions of regions that provide abundant prey (sand hills) *vs.* those that provide suitably stable hibernacula (rodent burrows in compacted clay soils). Snakes in the CO population were found aboveground at ambient temperatures of 12–44 °C ($\bar{x}$ = 26.4 °C; Wastell and Mackessy 2011), and Hobert *et al.* (2004) reported that they are active from 14 °C to 30 °C at an average ambient temperature of 22.1 ± 2.5 °C.

Figure 7. A litter of *Sistrurus tergeminus* (Western Massasauga) found on 1 September 2016, on Ash Flat, Graham Co. Six neonates were observed and a gravid *Crotalus cerberus* (Arizona Black Rattlesnake) was found in the same rock pile. Photo by Norman Dong.

■ **Reproduction.** The reproductive biology of *S. catenatus* and *S. tergeminus* is summarized by Fitch (1970), Minton (1983), Seigel (1986), and Ernst and Ernst (2011). Goldberg and Holycross (1999) presented reproductive data for AZ and CO populations. Males underwent spermatogenesis from June through October. Mature sperm occurred in the *vas deferens* and the kidney had enlarged sexual segments April–October, suggesting males are capable of inseminating females throughout this period. The smallest reproductively active male measured 280 mm SVL. Goldberg and Holycross (1999) reported females with vitellogenic follicles or embryos April–August and suggested that births occur from late August through late September, which is later in the year than most AZ rattlesnakes (Fig. 7). The smallest reproductively active female was 329 mm SVL. Only 15% of 46 adult females from AZ and CO were reproductively active in the study by Goldberg and Holycross (1999). Based on this percentage and reproductive data from six radio-tagged snakes in CO, Wastell and Mackessy (2016) concluded that female *S. tergeminus* reproduce biennially; their size/age class distribution data suggested individual females might only reproduce once in their lifetime in the CO population (Wastell and Mackessy 2016).

Wastell and Mackessy (2016) reported male-male combat on 27 April in the CO population. Chiszar *et al.* (1976) described the courtship behavior of captive *S. t. tergeminus*. Captives from AZ mate in both spring and fall; however, courtship and mating remain unobserved in the wild in AZ (Lowe *et al.* 1986). In adjacent states, a pair was observed courting on 9 June at Mescalero Sands, NM (Heupel *in* Schuett *et al.* 2016a); in CO, a pair was found together on 24 April, and one instance of courtship and two instances of copulation were observed in September (Mackessy 2005; Wastell and Mackessy 2016). Goldberg and Holycross (1999) reported litter sizes in AZ and CO of 4–8 ($\bar{x} = 5.8$ ± 1.7, $n = 4$). Two captives collected in AZ gave birth to five and seven young (Lowe *et al.* 1986). In CO, six radio-tagged females gave birth from 14 August to 9 September ($\bar{x}$= 23 August) to litters of 2–5 offspring ($\bar{x} = 3.3$ ± 1.2). Females attended their young for 5–7 days ($\bar{x} = 5.7$) after giving birth (Wastell and Mackessy 2011, 2016). Also in CO, a 380 mm SVL female (DOR) collected 30 May contained five vascularized ova, and a female collected 24 July gave birth in captivity on 24 August to seven young that averaged 148 mm SVL and 3.46 g (Hobert *et al.* 2004). Four YOY caught in AZ measured 162, 166, 167, and 176 mm SVL and weighed 3.9, 5.1, 4.9, and 3.4 g, respectively (Goldberg and Holycross 1999). Hobert *et al.* (2004) reported a mean SVL of 191.4 mm ± 16.0 for 23 YOY collected in the field from 3 September to 15 October. Neonates born in captivity to females collected in the wild in CO ($n = 9$) averaged 155 mm SVL and 3.97 g (Wastell and Mackessy 2016).

■ **Remarks.** *Sistrurus tergeminus* has been protected in AZ by a year-round closed hunting season since 1 January 1989. Mackessy (2005) reviewed the conservation status of *S. t. edwardsii*, with a focus on CO populations. Snider and Bowler (1992) recorded a maximum longevity of 20 yr, 5 d in captivity. However, a male collected as a large adult in the San Bernardino Valley on 19 July 1987 died on 19 July 2018, after exactly 31 years in captivity (B.L. Starrett, pers. comm.). Population-specific data on demography and growth for the CO population appear in Hobert *et al.* (2004) and Wastell and Mackessy (2016). Field studies of *S. t. tergeminus* have been largely omitted from this account because populations assigned to this putative subspecies substantially differ in many aspects of their natural and life history from those historically assigned to *S. t. edwardsii*. However, Minton (1983), Campbell and Lamar (2004), and Ernst and Ernst (2011) provided thorough literature reviews of *S. catenatus* (*sensu lato*). Since the publication of these reviews, Patten (2006) and Patten *et al.* (2016) have published novel information on NE populations.

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