# *Sonora semiannulata*

## Western Groundsnake

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**Figure 1.** *Sonora semiannulata* (Western Groundsnake) from near Florence, Pinal Co. Photo by Berkeley Martineau.

**Taxonomy.** *Sonora semiannulata* was described by Spencer F. Baird and Charles Girard (1853) from a specimen collected during the United States–Mexican boundary survey that occurred between 1848 and 1855 (Goetzmann 1958; James 1969). Although Baird and Girard attributed the collection to Colonel James D. Graham, head of the scientific corps, the report's preface specifies that the actual collector was John H. Clark (Baird and Girard 1853; Degenhardt *et al.* 1996). Although the holotype's collection date is unknown (Frost 1983b), Graham was only present during 1851 and 1852 (Goetzmann 1958; James 1969), suggesting that this specimen was collected in one of those years. The type locality in the description was "Sonora, Mexico." Stickel (1943) restricted the type locality to the vicinity of the Santa Rita Mountains of southern AZ, based on historical records from the expedition. However, this locality was in the Mexican state of Sonora prior to the Gadsden Purchase in 1854.

*Sonora semiannulata* displays a highly polymorphic color pattern that has long confounded taxonomists. Specimens now referable to *S. semiannulata* were initially placed into separate genera, such as *Lamprosomum episcopum* (Kennicott in Baird 1859) [then as *Contia episcopa torquata* (Cope 1880) and *Contia nuchalis* (Schenkel 1901)], *Contia taylori* (Boulenger 1894), and *Contia isozona* (Cope 1867b). These names were synonymized into *S. semiannulata* by Van Denburgh (1922) and Ortenburger (1923b). In a systematic revision of the genus, Stickel (1938) recognized six species in the genus *Sonora*: *S. episcopa* (Kennicott in Baird 1859), *S. miniata* (Stickel 1938), *S. mosaueri* (Stickel 1938), *S. occipitalis* (Hallowell 1854), *S. semiannulata* (Baird and Girard 1853), and *S. taylori* (Boulenger 1894). *Sonora miniata* had two subspecies (*linearis*, *miniata*), and *S. semiannulata* had three subspecies (*blanchardi*, *gloydi*, *semiannulata*). The type localities for the defunct *S. miniata* ("3 miles north of Mesa") and *S. gloydi* (Bright Angel Trail, Grand Canyon) are in AZ.

Five years later, Stickel (1943) recognized only *S. episcopa*, *S. mosaueri*, and *S. semiannulata* and placed *occipitalis* in the genus *Chionactis*. He recognized four subspecies of *S. semiannulata* (*blanchardi*, *isozona*, *linearis*, *semiannulata*) and moved *taylori* to subspecific status under *S. episcopa*. Klauber (1943a) added another species (*S. bancroftae*) to *Sonora* from Baja California. In his North American checklist, Schmidt (1953) recognized *S. episcopa*, *S. e. taylori*, *S. s. semiannulata*, *S. s. blanchardi*, *S. s. gloydi*, *S. s. isozona*, and *S. s. linearis*. Stebbins (1954, 1966) included *S. episcopa* and *S. semiannulata* in his field guides but did not include subspecies.

This taxonomy was greatly simplified by the morphological analysis of Frost and Van Devender (1979) and Frost (1983a), which collapsed all species and subspecies of *Sonora* that occur in the United States and Baja California into a single species with no subspecies (*S. semiannulata*). This arrangement was followed by some authors (Conant and Collins 1998; Stebbins 1985, 2003), while others still recognize populations found in south TX as a distinct subspecies, *S. s. taylori*, based on meristic characters (Werler and Dixon 2000; Crother 2012; Dixon 2013). Although recent molecular phylogenies (Davis Rabosky *et* *al.* 2016a, Cox *et al.* 2018) demonstrate that taxonomic revision is necessary, these changes do not affect *S. semiannulata* in AZ. Within AZ, however, there is a surprising amount of genetic diversity, with members of divergent molecular lineages in close geographic proximity, especially in Cochise, Pima, and Yavapai counties (Cox *et al.* 2018).

*Sonora semiannulata* is the type species of the genus *Sonora* and has three congeners that are found in central and western México (*S. aemula*, *S. michoacanensis*, and *S. mutabilis*). *Sonora aemula* in northwestern México is the sister species to *S. semiannulata* (Cox *et al.* 2012). Close evolutionary relationships between the genus *Sonora* and the genera *Chilomeniscus* (sandsnakes) and *Chionactis* (shovel-nosed snakes) have been proposed by some authors (Dowling 1975; Dowling and Duellman 1978), with *Chionactis* at one time considered synonymous with *Sonora* (Van Denburgh 1922; Stickel 1938). *Sonora* is usually placed in the colubrid snake tribe Sonorini with the genera *Chilomensiscus*, *Chionactis*, *Conopsis*, *Ficimia*, *Gyalopion*, *Pseudoficimia*, *Stennorrhina*, and *Sympholis* (Dowling 1975; Dowling and Duellman 1978). Some authors also include *Tantilla* and *Geagras*, and by extension, *Scolecophis* and *Tantillita* in the Sonorini (Savitzky 1983; Greene 1997; Holm 2008).

A recent molecular phylogenetic study discovered that *S. seminannulata* was not monophyletic and contained substantial genetic diversity (Cox *et al.* 2018). Four reciprocally monophyletic clades were geographically delimited, with one clade paraphyletic with regard to the rest of *S. semiannulata* (actually sister to *S. aemula*). These four clades corresponded closely to previously recognized species and subspecies of *Sonora* (Stickel 1938; Stickel 1943). Cox *et al.* (2018) proposed using *S. semiannulata* for snakes in the western US and northwestern Mexico (including all of AZ), *S. episcopa* (Variable Groundsnake) for snakes in the central US and northern Mexico, and *S. taylori* (South Texas Groundsnake) for the individuals found in TX south and east of the Balcones escarpment.

Cox *et al.* (2018) also discovered that *Sonora* was paraphyletic with regard to *Chionactis* and *Chilomeniscus*, with both of these genera nested within the genus *Sonora*. They resolved this paraphyly by placing *Chionactis* and *Chilomeniscus* in synonymy with *Sonora*. Thus, Cox *et al.* (2018) recognized 15 species of diminutive and often brightly colored snakes in a single genus (*Sonora*) that is distributed from central Mexico to the northwestern United States. These authors evaluated several other taxonomic rearrangements that resolved the paraphyly, but contended that synonymizing the genera, (1) best promotes future stability in this clade, (2) is consistent with historic taxonomy, and (3) highlights the biogeographic and ecological similarities among these 15 species (see Cox *et al.* 2018).

**Figure 2.** *Sonora semiannulata* (Western Groundsnake) from the Verde Valley, Yavapai Co. Photo by Andrew T. Holycross.

*Etymology.* The generic name *Sonora* was presumably coined in reference to the region of the type locality in Sonora, México. The specific name *semiannulata* (L. *semi*, half; L. *annulus*, ring) means "half-banded" and refers to the banding pattern of the holotype, in which the rings fail to cross the venter (Baird and Girard 1853).

**Description.** *Sonora semiannulata* is a small, medium-bodied species with relatively large eyes and a moderately blunt head shape (Figs. 1 and 2). Its body size in AZ is 210–345 mm SVL (Wright and Wright 1957; Ricards 1961; Ernst

**Figure 3.** *Sonora semiannulata* (Western Groundsnake) from along the Verde River, Maricopa Co. Photo by Trent R. Adamson.

and Ernst 2003). Sexual size dimorphism is minimal rangewide (Kassing 1960), and there is no documented size dimorphism in AZ (Goldberg 2001a). However, males have relatively longer tails than females (Clark 1966), with tail length >19% of TL in males and <19% in females (Ernst and Ernst 2003). The last three teeth on the maxillary bone are elongated and at least twice as long as the other teeth (Dowling and Duellman 1978). The hemipenis is a single, slightly bilobed, subcylindrical organ with a simple, oblique *sulcus spermaticus*; fleshy spines ornament the base (Dowling and Duellman 1978; Frost 1983b).

*Coloration and Pattern.* This species possesses an exceptional array of color polymorphism and color variation that occurs both within and among populations (Mulaik 1935; Frost and Van Devender 1979; Werler and Dixon 2000; Ernst and Ernst 2003; Cox and Davis Rabosky 2013; Davis Rabosky *et al.* 2016a). Although distinct color patterns have been described in numerous ways, the majority of this variation can be classified as discrete polymorphism for two dorsal color traits: a longitudinal red stripe and black crossbands. The presence or absence of either trait combines to create four distinct morphs: (1) red-striped (Figs. 3–5),(2) black-banded (Fig. 6), (3) both red-striped and black-banded (Figs. 7 and 8), and (4) uniform ground color with no distinctive markings (Fig. 9).

Additionally, there are two other polymorphic pattern elements that seem to be expressed independently of the red stripe or black bands on the body: a single (rarely two) black nuchal collar (or band) and a black cephalic cap. Ground color can vary considerably, from nearly black (Kassing 1960) to white or cream (CLC and ARDR, pers. obs.), with shades of tan, gray, reddish-buff, and brown being quite common (Curlis 2017). The degree of dark pigment on individual scales may also vary to such a degree that some snakes appear speckled, while others are unmarked.

**Figure 4.** *Sonora semiannulata* (Western Groundsnake) from the foothills of the Harcuvar Mountains, La Paz Co. Photo by William Wells.

**Figure 5.** *Sonora semiannulata* (Western Groundsnake) from the Harquahala Mountains, La Paz Co. Photo by Don S. Sias.



Additionally, the red stripe can vary in both intensity and width (Figs. 3–5), and in western TX and Baja California, some individuals possess gray rather than black bands (Fig. 10; Klauber 1943a; Grismer 2002). The number of bands can vary from 14 to 28. They range from saddles that do not cross the ventral scales to full rings that completely encircle the venter.

In addition, some individuals possess rare pattern aberrations. Bands may be incomplete or missing, or may fade sequentially from well-developed bands near the head to complete absence at the tail. Rarely, individuals give the illusion of a dorsal stripe that lacks red pigment due to a high level of black markings on the sides that is absent along the dorsal midline. One potential albinistic male specimen (ASU 4563) was collected in August 1962 from an irrigation ditch in Phoenix and was described in life as "chalk-white, with a faint pink pattern" that seems to be the striped phase (Echternacht 1964; ARDR, pers. obs. of preserved specimen). Hatchlings emerge patterned exactly like adults; although one author reported that a dorsal red stripe appeared several days after hatching (Staedeli 1964), this is probably just a change in the detectability of the stripe as juveniles grow.

Although all four color morphs (and much of the ground color variation) occur in AZ, there are distinct patterns in the distribution of morphs across the state (Fig. 11). Santa Cruz Co., especially the area near Patagonia and Sonoita, is unique among all populations across the entire species in that it appears fixed for the black-and-red morph. The unmarked uniform morph is rare to absent across the entire southern portion of the state, as it does not reach appreciable frequencies until as far north as Pinal and Maricopa counties. Pima, Cochise, and Yuma counties are dominated by red-striped and black-and-red morphs, while most of central AZ (especially the greater Phoenix metropolitan area) is highly polymorphic for all four morphs. However, the population at Grand Canyon has been described as containing only black-banded morphs (Stickel 1938). Although the authors' collection efforts support this conclusion, not enough specimens have been collected to rule out the presence of additional morphs, especially because striped morphs are common farther downstream along the Colorado River (southern NV and southeastern CA) and black-and-red morphs dominate farther upstream (southern UT).

*Scutellation.* This snake exhibits a standard colubroid arrangement of lateral head scales, with 2 internasals, 2 prefrontals, 1 frontal, and 2 parietals, 1 nasal, 1 loreal, 1 preocular, 1 supraocular, and usually 1+2 temporals. Generally, there are 7 (sometimes 6) supralabials on a side and 7 (sometimes 6) infralabials. In AZ, dorsal scale rows are 14 (13–16) anteriorly, 15 (14–16) at mid-body, and 14 (14–16) distally. This dorsal scale reduction to 14 occurs in the posterior 70% of the body prior to the cloaca. Body scales are smooth with no apical pits. Ventral scale (Dowling method) counts (126–168 in males and 136–186 in females) and subcaudal counts (39–59 in males and 31–51 in females) vary geographically. In AZ, ventral counts are 147–168 in males and 157–183 in females, and subcaudals are 41–57 in males and 37–54 in females. The cloacal scale and all subcaudals are divided. Squamation in *S. semiannulata* is summarized from Stickel (1938, 1943), Wright and Wright (1957), Frost and Van Devender (1979), Frost (1983a), Werler and Dixon (2000), and Ernst and Ernst (2003). There are no comparable data for AZ snake populations.

*Similar Species.* The uniform morph of *S. semiannulata* may be confused with several other small, uniformly colored snakes in AZ, especially when a black cap is present (Fig. 2). *Sonora semiannulata* may be distinguished from snakes of the genus *Tantilla* by general appearance (*Tantilla* snakes in AZ have a flattened head, small eyes, are more slender and may have a reddish venter compared to *S. semiannulata*), the presence of a loreal scale in *S. semiannulata* (absent in *Tantilla*), and higher gular scale count (generally >22) in *S. semiannulata*. We caution that some individuals of *Tantilla* may possess oddly shaped or split preoculars that may be misidentified as a loreal scale. *Diadophis punctatus*, although similar in size, shape, and color, is easily distinguished by the presence of a pale nuchal ring (usually) and reddish to yellow ventral surface, particularly on the tail. Black-banded and black-and-red morphs of *S. semiannulata* may be confused with a number of banded species of similar size and color: *Chilomeniscus cinctus*, *Chionactis annulata*, *C. occipitalis*, *C. palarostris*, *Gyalopion quadrangulare*, young *Lampropeltis splendida* and *L. californiae*, and young *Rhinocheilus lecontei*. All of these species, with the exception of *L. californiae* and *L. splendida*, may be easily distinguished from *S. semiannulata* by their modified or enlarged rostrum. Juvenile *L. californiae* and *L. splendida* have a single cloacal scute, whereas it is divided in *S. semiannulata*.

**Distribution and Abundance.** *Sonora semiannulata* occurs over much of the western United States and northern México (Frost 1983b). The eastern extent of the range is in the glades of southwestern MO and northwestern AR, and the western portion into southern KS, OK, TX, and the northern region of the Mexican state of Tamaulipas. The center of its range is in NM, AZ, UT, NV, and northern regions of the Mexican states of Coahuila, Nuevo León, Chihuahua, and Sonora. There are isolated populations of *S. semiannulata* in southeastern CO (Lambert and Reid 1981), north-central KS (Russell Co.; Brennan 1934) and the Mexican state of Durango (Frost 1983b). In the western part of its range, *S. semiannulata* extends from the tip of the Baja Peninsula in the Mexican state of Baja California Sur northward into the Mojave Desert and east of the Sierra Nevada in CA (Grismer 2002). *Sonora semiannulata* also occurs on the islands of San José and San Marcos in the Sea of Cortés (Cliff 1954; Grismer 2002). The northernmost location where *S. semiannulata* occurs is in a disjunct population in the Snake River Valley of southeastern OR and southwestern ID (Storm 1947; Diller and Wallace 1989). Throughout its range, *S. semiannulata* is found from sea level to *ca.* 2,000 m ASL.

*Sonora semiannulata* occurs throughout much of AZ (Map 28), but has not been vouchered in Apache, Greenlee, or Navajo counties (McKee and Bogert 1934; Cowles and Bogert 1936; Gates 1957; Tanner 1958; Cogan 2011). Because *S. semiannulata* is also absent from all NM counties west of the Rio Grande Basin except for the southernmost counties (Hidalgo and Grant), this lack of records may represent true absence (or at least extreme rarity), especially for Apache and Navajo counties, with the high elevations of the Mogollon Rim and Colorado Plateau creating an effective barrier to dispersal. More sampling is needed in the northern part of AZ, NM, and southern UT, which may be logistically challenging. However, *S. semiannulata* is expected to occur in southern Greenlee Co., particularly along the Gila River. In general, *S. semiannulata* in AZ follows the major river corridors: it is especially common along the Colorado, Verde, Gila, Salt, Santa Cruz, and San Pedro river valleys. However, it can also be found in mountain ranges (especially along washes) and at low densities in grasslands throughout the state below its elevational limit. Although present in areas with sand, *S. semiannulata* seems to be replaced by *Chionactis* in areas dominated by large sand dunes, especially along the northern rim of the Gran Desierto region. We have found *Sonora* in the Patagonia Mountains of Santa Cruz Co., the SR 80 corridor northeast of Douglas, the Mazatzal Mountains northeast of Phoenix, the Tortolita Mountains northwest of Tucson, just south of Sedona, southeast of Bagdad, and along the Bright Angel Trail in Grand Canyon.

*Questionable Localities.* Two specimens (UAZ 26371–72), both collected on 9 June 1951 from "Wupotkai Nat'l Mon" (according to their field tags), are 90 km from the nearest specimens to the NW in Grand Canyon and 80 km from the nearest specimens to the SW in Sedona (Persons 1999). Although the Wupatki specimens are isolated records, and the species was not detected during five years of intensive annual herpetological surveys at Wupatki National Monument (Persons 2001, Persons and Nowak 2006), the handwritten tags attached to the specimens provide reasonably specific locality information, and we regard them as valid. We have received reports of unvouchered sightings of *S. semiannulata* all the way up the Colorado River from Yuma through Page, but vouchered material is necessary to confirm presence within the gaps in their documented distribution along the river and in large portions of Grand Canyon.

*Status and Trends. Sonora semiannulata* appears to vary in abundance across its geographic range (Force 1930; Wood 1945; Slevin 1950; Fitch 1993; Jones *et al.* 2011b), but is only considered a species of conservation concern in states at the periphery of its geographic range (AR and OR), and seems to persist or even thrive in some urban and suburban settings (Smith *et al.* 2008a). In AZ, some historically abundant populations may have been extirpated due to urban sprawl or changing agricultural practices (*e.g.*, near Laguna Dam, Imperial Co., CA, and adjacent areas of AZ, Wood 1945; Slevin 1950; CLC and ARDR, pers. obs.). Although present in the adjacent Avra Valley, populations are absent from much of the greater Tucson Basin (Rosen 2004), which may be due to natural absence or extirpation due to development. The Phoenix metropolitan area has more records by far than anywhere else in the state, possibly reflecting a true relative abundance difference even in light of a probable sampling bias.

**Habitat.** Generally, *S. semiannulata* occurs in open, semiarid to arid habitats throughout its range. In mesic areas, *S. semiannulata* is found in drier microhabitats; it is conversely associated with moister microhabitats in arid areas (Klauber 1939c). Throughout its range, it is most abundant, or at least most easily collected, in rocky areas (Force 1930; Axtell 1959; Diller and Wallace 1989). In AZ, *S. semiannulata* occurs in Semidesert Grasslands; Sonoran, Chihuahuan, and Mojave desertscrub habitats; and in red-rock canyon lands of the Great Basin (Cowles and Bogert 1936; Gates 1957; Jones *et al.* 2011b). In the more arid parts of AZ, rocky hillsides along rivers and temporary streams can have particularly high densities of these snakes. Jones (1981) found them abundant in mixed juniper, desert grassland, and palo verde–saguaro habitats in west-central AZ. They also occur in thornscrub, pinyon-juniper woodland, and oak-pine forest. *Sonora semiannulata* can also be common in urban settings such as Phoenix and Yuma, with many records from backyards and

**FIGURE 6.** *Sonora semiannulata* (Western Groundsnake) from Bright Angel Trail, Grand Canyon, Coconino Co. Photo by Christian L. Cox.

**FIGURE 7.** *Sonora semiannulata* (Western Groundsnake) from the McCloud Mountains, Yavapai Co. Photo by Randall D. Babb.

neighborhoods in the greater Phoenix metropolitan area (Smith *et al.* 2008a).

**DIET AND FORAGING BIOLOGY.** These snakes consume a great variety of hard-bodied arthropods across their geographic range (Kassing 1960; Fong 1980; Degenhardt *et al.* 1996; Ernst and Ernst 2003), including arachnids, centipedes, and diverse insects. Carpenter (1958) reported that a large male regurgitated a medium-sized scorpion and another snake regurgitated two beetle larvae and a moth. Scolopendramorph centipedes have been reported in the diet by Anderson (1965) and in captivity by Holm (2008). Kassing (1960) reported that 39 of 81 snakes from OK that had been immediately preserved upon capture contained identifiable prey remains. The predominant prey were spiders, including egg masses, and many of these were of the family Lycosidae (wolf spiders). Centipedes (*Lithobius*) and scorpions (family Buthidae) were also prominent prey; additional items included the insect orders Coleoptera, Lepidoptera, Hymenoptera, and Orthoptera. Holm (2008) reported 29 prey from an undisclosed number of snakes; among these were 11 spiders or solpugids, 8 orthopterans, 4 "other invertebrates," 3 scorpions, and 3 beetle larvae. Holm (2008) suggested that specialization on arachnids is primitive for the clade of Sonorini that includes *Sonora*. The only records of predation on vertebrates are *Coleonyx* (banded geckos), *Holbrookia* (lesser earless lizards), *Aspidoscelis* (whiptail lizards; Degenhardt *et al.* 1996; Ernst and Ernst 2003) and hatchling *Urosaurus ornatus* (Ornate Tree Lizard; Holm 2008). In captivity, these snakes eat many live arthropods, including crickets, grasshoppers, spiders, and harvestmen, as well as dead spiders (CLC and ARDR, pers. obs.) and dead skinks (Ernst and Ernst 2003). The only diet record from AZ was a *S. semiannulata* from near Fort Huachuca that died after feeding on poisoned grasshoppers (poison not reported; Woodin 1953).

The feeding biology of *S. semiannulata* is not well known. McCallion (1945) and Kassing (1960) reported observations by Phillip M. Harter of *S. semiannulata* feeding on scorpions: "In three instances the scorpion had been grasped by the tail." Fong (1980) observed similar behavior in an unsuccessful predatory event. Additionally, these snakes engage in pheromone-trailing behavior that may help them detect and consume their arthropod prey (Gehlbach *et al.* 1971). In certain parts of their range, they can be commonly found crossing roads at night, suggesting they forage nocturnally. These snakes feed frequently in captivity (CLC and ARDR, per. obs.), and due to their small size (and the small relative size of their invertebrate prey), it is likely that *S. semiannulata* feed frequently in the wild.

**Figure 8.** *Sonora semiannulata* (Western Groundsnake) from Gilbert, Maricopa Co. Photo by Randall D. Babb.

**Figure 9.** *Sonora semiannulata* (Western Groundsnake) from Phoenix, Maricopa Co. Photo by Thomas R. Jones.



*Sonora semiannulata* has several anatomic features that may play a role in its foraging biology. Snakes in this genus possess cutaneous touch corpuscles (Jackson 1977) that may be used for prey sensing and manipulation. Some authors suggest that this species uses enlarged and grooved rear maxillary teeth and venomous saliva to help subdue prey (Ernst and Ernst 2003). There have been no morphological, biochemical, or feeding behavior studies of *S. semiannulata* to confirm this hypothesis, but it would be an interesting area for future research.

**Predators and Parasites.** *Sonora semiannulata* is likely prey for multiple vertebrate species that eat squamate reptiles, including carnivorous mammals, birds of prey, turtles, and other squamate reptiles (summarized in Webb 1970; Tennant 1984; Ernst and Ernst 2003). One of the more interesting records of predation on *S. semiannulata* (and the only record of predation by an invertebrate) is of a large *Scolopendra heros* (Giant Desert Centipede), which was observed killing and consuming an adult in west TX (Johnson *et al.* 2007). In AZ, documented predators include *Bassariscus astutus* (Ringtail, from a fossil midden of the Holocene; Mead and Van Devender 1981), *Kinosternon sonoriense* (Sonora Mud Turtle; Lovich *et al.* 2010), *Gambelia* (leopard lizards, M.J. Feldner, pers. comm.), *Crotalus cerastes* (Funk 1965b), and *Micruroides euryxanthus* (in captivity; Vitt and Hulse 1973; Veer *et al.* 1997). Clark (1968b) and Wiseman *et al.* (2019) reported four incidents of predation by *Lampropeltis californiae*. A headless, 185 mm *S. semiannulata* was recovered from the stomach of a field-collected adult male *Crotaphytus collaris* (Eastern Collared Lizard; Best and Pfaffenberg 1986). *Diadophis punctatus* consumed *S. semiannulata* in captivity (Storm 1947).

Research on parasites in *S. semiannulata* is sparse. A single study found *Oochoristica parvula* (cosmocercid nematodes), *Aplectana* spp. (ascarid nematodes), and *Spauligodon goldbergi* (oxyurid nematodes) in the intestines of *S. semiannulata*, the latter being described as a new species (Bursey and McAllister 1996). Hilman and Strandtmann (1960) reported the absence of the blood protozoan *Herpetozoon serpentium* in 12 specimens they examined from TX.

**Behavior.** *Sonora semiannulata* is most frequently encountered either by turning rocks or while crossing roads at dusk or night. Due to its secretive habits and occurrence on roads at night, *S. semiannulata* is considered primarily nocturnal (Tenant 1984; Degenhardt *et al.* 1996; Grismer 2002). These snakes are semifossorial. They often quickly attempt to escape into a nearby burrow or crack in a rock when

**Figure 10.** *Sonora semiannulata* (Western Groundsnake) from near Superior, Pinal Co. Photo by Jeffrey Martineau.

exposed (Strecker 1934; Minton 1959). Cavities under rocks may connect to deeper retreats. In fact, *S. semiannulata* possesses scale adaptations to fossorial locomotion (*e.g.*, posterior free margin of ventral scales; Jackson and Reno 1975) that reduce friction or provide traction points, but unlike other fossorial snakes, this species retains large and well-developed eyes.

Patterns of seasonal abundance vary geographically. In the east, it tends to be most common in the spring and early summer, while it seems to be active later in the summer in the western parts of its range (Strecker 1934; Kassing 1960; Reynolds 1982; Ruthven *et al.* 2002; Ryberg and Fitzgerald 2005). This may reflect actual geographic variation in activity patterns or variation in herpetological collection techniques from east to west. *Sonora semiannulata* is also found in association with several other small, semifossorial snakes, including *Hypsiglena*, *Salvadora*, and *Tantilla* species and *Rena humilis* within AZ and elsewhere (CLC and ARDR, pers. obs.).

*Sonora semiannulata* exhibits a number of antipredator behaviors. It can feign death by vigorous writhing, defecation, and musking, followed by immobility while lying on its back (Gehlbach 1970; Hillis 1977; Greene 1988). This behavior has been documented in response to both humans and ophiophagous snakes, and may effectively deter certain predators (Gehlbach 1970; Hillis 1977). It may also hide its head in body coils and wave its tail as an apparent distraction (Tenant 1984). In response to snake attacks, it can twist vigorously and form a loop while biting its own tail, in an attempt to prevent consumption (Veer *et al.* 1997; R.D. Babb, pers. comm.). Finally, it may also engage in a contact-induced leaping behavior (Fong 1980), whereby it lifts its body violently off the substrate (sometimes entirely) in response to touching.

**Reproduction.** *Sonora semiannulata* is oviparous and reaches sexual maturity in both sexes at 230–300 mm SVL (around 1.5–2.5 years of age; Wright and Wright 1957; Carpenter 1958; Kassing 1960). Breeding occurs mostly in spring but may also take place in the fall (Kassing 1960). Males search for females and engage in combat consisting of biting, intertwining, and writhing behaviors (Kroll 1971; Broussard *et al.* 2020; Jantzi *et al.* in press). Courtship consists of head-to-head rubbing, the male biting the female on the neck, and more vigorous intertwining and writhing (Kassing 1960; Anderson 1965). Spermiogenesis in males occurs from March to October, and enlargement of the sexual kidney occurs from January through July (Goldberg 2001a).

Enlarged follicles in AZ females are present from April through July, and oviductal eggs have been found in June and July (Goldberg 2001a; Holm 2008). Gravid females gestate for around 30 days and lay clutches of 3–6 eggs (Kassing 1960; Staedeli 1964; Tenant 1984; Ernst and Ernst 2003). In OK, Carpenter (1958) reported oviposition of a clutch of three eggs on 17 June and a clutch of five eggs over a period of five days, 19–23 June. Holm (2008) listed clutch sizes of 3–6 ($\bar{x}$ = 4.2, $n$ = 52) based on reports from the literature and original data. In AZ, the clutch size is 6–12; eggs measure 17–29 x 8 mm and weigh 0.9–1.3 g; hatchlings are 105–125 mm TL and 0.3–0.4 g in weight (Goldberg 2001a; R.D. Babb, pers. comm.). Total lengths of four hatchlings from CA were 110–125 mm (Staedeli 1964).

**REMARKS.** Fossil records of *S. semiannulata* are known from the Late Pleistocene and Early Holocene, mostly from AZ in Grand Canyon and near Picacho Peak (Van Devender *et al.* 1977; Van Devender and Mead 1978; Mead and Van Devender 1981; Johnson 1986; Van Devender *et al.* 1991a). *Sonora semiannulata* is sometimes killed in fires; Simons (1989) found three snakes that were killed by a prescribed fire near the confluence of the Salt and Verde rivers.

All *Sonora* species, including *S. semiannulata*, are coralsnake mimics (Savage and Slowinski 1992; Greene 1997; Brodie III and Brodie Jr. 2004). They possess all of the key features typical of other mimetic species, including (1) geographic ranges with broad areas of sympatry with coralsnakes, (2) highly visible red and black coloration, and (3) conservatism across the genus in black-and-red coloration, suggesting a long evolutionary history of mimicry (Cox *et al.* 2012; Davis Rabosky *et al.* 2016b). Even though the black-and-red morph of *S. semiannulata* is not a complete tricolor (black, red, and yellow) pattern, mimetically colored individuals are routinely mistaken for coral snakes, even in places far outside the range of coral snakes (Erwin 1925), and treated as venomous (once purposefully sucked into a vacuum cleaner by the staff at Montezuma Castle National Monument Visitor Center, UAZ-55970).

The genetic control of color pattern in *S. semiannulata* is unknown, although red and black coloration are controlled by separate loci (Davis Rabosky *et al.* 2016a) and color pattern is not controlled by sequence variation in the Mc1r gene (Cox *et al.* 2013). Color polymorphism extends throughout the genus (Echternacht 1973; Cox *et al.* 2012), as black and red, solid red, and tricolor morphs are found in the three Mexican congeners (*S. michoacanensis*, *S. mutabilis*, and *S. aemula*). Although *S. semiannulata* is unique among *Sonora* in that one of the morphs (the uniform morph) possesses neither black nor red coloration, this color morph is also common in the close relative *Chilomeniscus stramineus* in Baja California (CLC and ARDR, pers. obs.). Geographic variation in the presence and frequency of color morphs in *S. semiannulata* is governed by selection that varies over time and space (Cox and Davis Rabosky 2013). The exact dynamics and effects of color variation within the Sonorini are an area of active research.

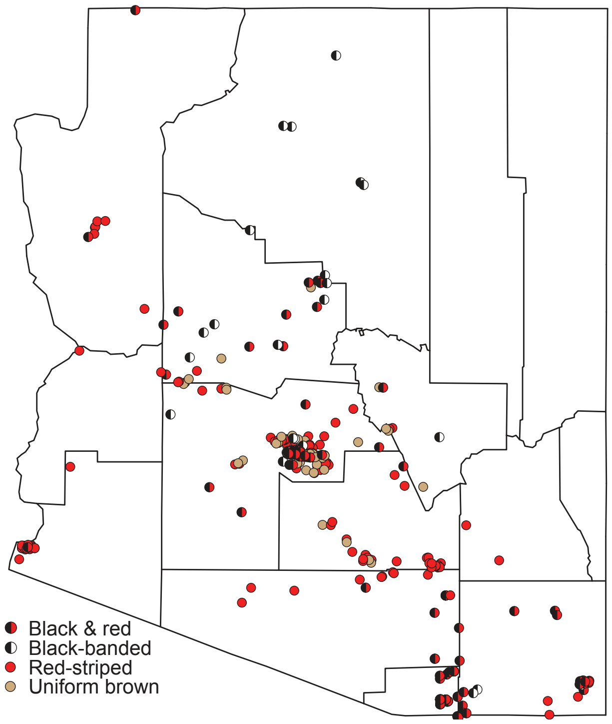


**FIGURE 11.** Distribution of color morphs for 530 vouchered *Sonora semiannulata* (Western Groundsnake) from AZ examined by the authors. Not all vouchered localities for *S. semiannulata* in AZ are included because the authors did not examine the supporting specimens (see Map 28 for a complete distribution of *S. semiannulata* in AZ). Multiple specimens georeferenced to the same locality have been slightly jittered to allow the display of overlapping points (*e.g.*, for Phoenix and Yuma). Illustration by Alison R. Davis Rabosky.

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