

Crotalus viridis

PRAIRIE RATTLESNAKE

Ryan P. O'Donnell, Trevor B. Persons,
Erik W.A. Gergus, and Andrew T. Holycross

TAXONOMY. *Crotalus viridis* was described as *Crotalinus viridis* by Rafinesque (1818) from a specimen collected by "Mr. Bradbury" from "the Upper Missouri." Smith and Taylor (1950) suggested, without comment, "Gross, Boyd County, Nebraska" as the type locality, and Schmidt (1953) inexplicably listed the type locality as the "vicinity of Kansas City, Missouri," a location that can hardly be considered to be along the "upper" Missouri River and is also outside the known range of *C. viridis*. Holycross *et al.* (2008) examined John Bradbury's (1817) account of his travels up the Missouri River and determined that Rafinesque's (1818) description is based upon a skin Bradbury collected on 21 June 1811 in the vicinity of Little Heart Flats, Morton Co., ND. They therefore restricted the type locality to "the prairies between the Cannonball and Heart rivers, within 40 km of the Missouri River in North Dakota" and pointed out that a type was never designated, and that the type material appears to be lost (Holycross *et al.* 2008).

Crotalus viridis is currently considered monotypic (*e.g.*, Crother 2017). Among previously described subspecies in the *C. viridis* complex (see below), only *C. v. viridis* (Prairie Rattlesnake) and *C. v. nuntius* (Hopi Rattlesnake) are included within *C. viridis* as currently recognized. *Crotalus v. nuntius* was described (as *C. confluentus nuntius*) by Klauber (1935a) from a specimen (LMK 3105, now SDNHM 3105) collected by R.L. Borden on 9 August 1930 at Canyon Diablo, Coconino Co., AZ. Klauber (1935a) was hesitant to designate *C. v. nuntius* as a subspecies because its overall pattern (*e.g.*, edges of the dorsal blotches, head markings, and form of the tail rings) was similar to that of *C. v. viridis*. However, he felt that conspicuous size and color differences between the two, as well as significant differences in scale counts, warranted their separation. Exemplifying the difference



FIGURE 1. *Crotalus viridis* (Prairie Rattlesnake) from the vicinity of Moenkopi Wash, south of its confluence with Hamblin Wash, Coconino Co. Photo by Brendan O'Connor.

in size, the smallest pregnant *C. v. viridis* from Colorado ($n = 149$) was 588 mm TL, whereas the smallest pregnant *C. v. nuntius* ($n = 6$) was only 395 mm TL. Previous names for *C. viridis* include *Crotalurus viridis* (Rafinesque 1820), *Crotalus confluentus* (Say in James 1822), *Crotalus lecontei* (Hallowell 1852), and *Caudisona confluenta* (Cope 1867b). Klauber (1936a) placed all subspecies of *Crotalus confluentus* (the then-prevailing species name) into *C. viridis*.

After a long period of relative taxonomic stability through much of the twentieth century, during which *C. viridis* was considered a single polytypic species with nine subspecies (*abyssus*, *caliginis*, *cerberus*, *concolor*, *helleri*, *lutosus*, *nuntius*, *oreganus*, and *viridis*; *e.g.*, Klauber 1972, Stebbins 2003), systematic research on the Western Rattlesnake (*C. viridis sensu lato*) species complex has produced a number of proposed taxonomic changes over the past few decades. Attempts to deduce phylogenetic relationships using various phenetic methods inherently produced suspect results (*e.g.*, Brattstrom 1964; Klauber 1972; Foote and McMahon 1977; Aird 1984). In addition to morphological characters, Aird (1984) included venom elution profiles, blood proteins, and niches. His analyses provided support for well-defined genetic differentiation between subspecies of *C. viridis*, and he suggested that *concolor*, *lutosus*, and *viridis* were legitimate

biological species. Quinn (1987) first identified significant mtDNA divergence between eastern (*C. v. viridis* and *C. v. nuntius*) and western (the remaining seven subspecies) lineages but did not formally propose partitioning the complex into more than one species. Quinn (1987) did, however, propose that *C. v. nuntius* was not a valid subspecies, and subsumed it within *C. v. viridis*. Pook *et al.* (2000), Ashton and de Queiroz (2001), and Douglas *et al.* (2002) all obtained similar results with their mtDNA analyses. The latter two specifically proposed that the eastern clade (*C. viridis*) be partitioned from the western clade (*C. oreganus*), while Pook *et al.* (2000) recommended retaining the traditional taxonomy until publication of concordant nuclear or morphological evidence. All three studies also found *C. cerberus* to be sister to the remaining members of the western clade, although only Douglas *et al.* (2002) explicitly proposed elevating the taxon to species status. Douglas *et al.* (2002) also proposed elevating *C. o. abyssus*, *C. o. concolor*, *C. o. helleri*, and *C. o. lutosus* to species status, and they identified undescribed clades within *C. o. lutosus* and *C. o. oreganus* that they suggested may represent new species. Crother (2017) cited congruence among these three studies in recognition of three species in the complex (*C. cerberus*, *C. oreganus*, and *C. viridis*).

Goldenberg (2013) used species tree inference and simultaneous multilocus coalescent-based species delimitation to examine sequence data for five nuclear introns and one mitochondrial gene from throughout the *C. viridis* complex and concluded that both *C. cerberus* and *C. viridis* should be recognized as distinct species. In addition, Goldenberg (2013) concluded that *C. oreganus* should be subdivided into four species: *C. helleri* (including *C. o. caliginis* and *C. o. helleri*), *C. lutosus* (including *C. o. abyssus*, *C. o. concolor*, and *C. o. lutosus*), *C. oreganus* (including *C. o. oreganus*, in part), and an undescribed species currently part of *C. o. oreganus*. Similar to Douglas *et al.* (2002), Goldenberg's (2013) sampling was not sufficient to delineate the geographic distribution of the undescribed species or propose specific

taxonomic changes to *C. o. oreganus*. Goldenberg (2013) found *C. oreganus* from the Pacific Northwest to be sister to a clade containing *C. o. lutosus*, *C. o. helleri*, and the undescribed species; this undescribed species, from central CA, was sister to *C. o. helleri*. However, Schneider (1986) found extensive phenotypic intergradation between *C. o. helleri* and *C. o. oreganus* in southern and central CA in the region of Goldenberg's (2013) hypothesized species divide between *C. o. helleri* and the undescribed species, suggesting that if found to be distinct from *C. o. oreganus*, this undescribed form may be conspecific (or consubspecific) with *C. o. helleri*. Although Crother (2017), citing Douglas *et al.* (2002), did not recognize *C. v. nuntius*, Goldenberg (2013) recommended continued recognition of the taxon because she found it to be mitochondrially monophyletic and nested within *C. v. viridis*, and suggested that it may therefore be in the process of lineage divergence or speciation.

Davis *et al.* (2016a) analyzed mtDNA and geometric morphometric data on head shape in the complex and recognized six species: *C. viridis* (including *C. v. nuntius*), *C. cerberus*, *C. concolor*, *C. helleri* (including *C. o. caliginis*), *C. lutosus* (including *C. o. abyssus*), and *C. oreganus*. Although *C. o. abyssus* is among Arizona's most beloved charismatic megafauna, it has weak support as a distinctive taxon, being nested within *C. o. lutosus* in cladograms presented by Pook *et al.* (2000), Ashton and de Queiroz (2001), Douglas *et al.* (2002), and Goldenberg (2013). In addition, Davis *et al.* (2016a) were unable to separate the two based on head shape, leading them to subsume *C. o. abyssus* within *C. o. lutosus*. The earlier proposal by Douglas *et al.* (2002) to elevate *C. o. abyssus* to species level was presumably based on the expectation that one of their recovered *C. o. lutosus* mtDNA haplotype clades (L3) would also merit separate species status, and would thus remove *C. o. lutosus* from paraphyly.

With regard to *C. cerberus*, Goldenberg's (2013) results were similar to those of previous researchers in strongly supporting it as a sister group to *C. oreganus* in a mitochondrial gene tree but diverged from previous studies in also



FIGURE 2. *Crotalus viridis* (Prairie Rattlesnake) from the vicinity of Hunt Valley, Apache Co. Photo by Andrew T. Holycross.

providing weak support for *C. cerberus* as the sister group to *C. viridis* when using a multilocus species tree approach. Goldenberg explained this apparent incongruity by hypothesizing either rapid or nearly concurrent divergence of the three lineages leading to *C. viridis*, *C. cerberus*, and all remaining species, or by recent gene flow between *C. cerberus* and *C. v. nuntius*. The latter hypothesis was rejected partly on the basis of “geographical isolation” of the two groups, although their close approach to each other in the Walnut Canyon area east of Flagstaff suggests current or recent gene flow is possible (Nowak and Schofer 2006; Persons and Nowak 2006). The gene flow hypothesis may be supported by the discovery of an individual from western AZ nested within the *C. v. nuntius* mtDNA clade, which Goldenberg (2013) ascribed to mitochondrial introgression. Feldner *et al.* (2016a) provided an exhaustive discussion of the morphological

variation and genetic affiliations of *C. cerberus* and *C. o. abyssus* individuals from western AZ. One of us (ATH) has examined many individual snakes and specimens from the Colorado Plateau, particularly in the Grand Canyon region, and has seen animals that appear to be morphologically intermediate between *C. cerberus* and *C. o. abyssus* as well as between *C. cerberus* and *C. viridis* in relatively narrow contact zones. Examination of museum specimens from northern AZ in areas of possible syntopy between *C. cerberus* and *C. viridis* suggests that where introgression appears to be occurring, it is limited to narrow contact zones that have not been exhaustively sampled in phylogenetic studies.

More recently, Schield *et al.* (2019) used both mtDNA and nuclear genetic data to assess gene flow and demographic history of the *C. viridis* complex and concluded that current diversity is largely the result of allopatric divergence followed

by secondary contact with widespread introgression, with reproductive isolating mechanisms insufficient to prevent introgression even among anciently divergent lineages. For example, within the western clade they suggested that greater than expected nuclear genetic diversity in *C. o. abyssus* might be the result of gene flow into Grand Canyon from adjacent *C. cerberus*, *C. o. concolor*, *C. o. lutosus*, and/or *C. v. nuntius* (Schield *et al.* 2019). In contrast, within the eastern clade, Schield *et al.* (2019) found evidence for divergence with continuous gene flow between *C. v. viridis* and *C. v. nuntius* and inferred that differentiation between populations of *C. viridis* is a result of isolation-by-distance, a finding that agrees with Klauber’s (1935a) observations of clinal variation between the forms in eastern AZ. Schield *et al.* (2019) did not make taxonomic recommendations, and their finding that the evolutionary history of the *C. viridis* complex does not fit a traditional bifurcating tree model, but instead reflects a complex history of divergence and introgression, suggests that debate over species limits in the complex will continue.

ETYMOLOGY. The generic name *Crotalus* (Gr. *krotalon* or L. *crotalum*, a clapper or castanet) refers to the rattle. The specific name *viridis* (L. *viridis*, green) is in reference to dorsal coloration in some individuals. The subspecific name *nuntius* (L. *nuntius*, messenger; Brown 1956) refers to the Hopi snake dance in which these snakes are considered messengers to the gods of the underworld (Klauber 1935a).

■ **DESCRIPTION.** *Crotalus viridis* is a moderately large rattlesnake throughout most of its range, with the largest individual reported by Klauber (1972) from MT, measuring 1,448 mm TL. In AZ, however, individuals seldom exceed ~900 mm TL (Lowe *et al.* 1986), and most adults measure ~600–750 mm TL (TBP, pers. obs.). The smallest snakes are found in the Winslow and Holbrook areas of the Little Colorado River Valley, Navajo Co., where Klauber (1935a) considered *C. v. nuntius* to be most typical. The largest specimen

from this region measured 732 mm TL (Klauber 1935a, 1972). Throughout its range, *C. viridis* tends to be larger in cooler and more seasonal areas, opposite the trend in *C. oreganus* (Ashton 2001).

Relative to that of other rattlesnake species, including members of the western clade of the *C. viridis* complex, the head of *C. viridis* is not particularly wide (Fig. 1), and is described by Davis and Douglas (2016) as being “egg-shaped” (contrasted with the “spear-shaped” head of *C. cerberus* and *C. oreganus*). Klauber (1972) does not include ranges or sample sizes but reports relative tail lengths (as a proportion of TL) of 7.5% and 5.3% for *C. v. viridis* males and females, respectively, and 7.7% and 5.5% for *C. v. nuntius* males and females, respectively. Although relative tail length averages longer in males, overlap is great enough that these characters are by themselves unreliable as an indication of sex (Quinn 1979; Rothe-Groleau *et al.* 2018). The rattle grows at approximately 1.5 segments per year in Kansas (Fitch 1985a), but growth rates in warmer climates like AZ are expected to be greater due to a longer active season. A rattleless female *C. viridis* with no evidence of scarring or injury was reported from NE (Holycross 2000b); the condition was deemed congenital. Painter *et al.* (1999a) described a secondhand report of a captive rattleless female *C. viridis* that gave birth to a litter including a rattleless neonate. Fitch (1998) reported two adult *C. viridis* without rattles, but did not speculate on whether this was congenital or due to injury.

The hemipenis has moderately long lobes with a ratio of length to diameter of 2.5 for *C. v. viridis* and 2.2 for *C. v. nuntius* (Klauber 1972). Each lobe has a mean of 67 (*C. v. nuntius*) to 92 (*C. v. viridis*) large spines and 27 (*C. v. nuntius*) to 37 (*C. v. viridis*) fringes, and there are no medial spines (Klauber 1972). To our knowledge, the hemipenis of *C. viridis* has not been illustrated.

COLORATION AND PATTERN. Although the name *viridis* implies that green is the prominent color, greenish snakes are mostly found outside AZ.

Coloration is variable throughout the range (*e.g.*, Campbell and Lamar 2004), and often matches local substrate color (Figs. 2-7; Stebbins 2003). For example, in NM ground color varies from "light brown to a dusty yellowish tan" (Degenhardt *et al.* 1996), and although Hammerson (1999) did not describe color for CO snakes, the numerous photographs depict predominantly brownish-colored individuals. Klauber (1935a) described "typical" *C. v. nuntius* from the Little Colorado River Basin as pink, red-brown, brown, or gray-brown. Klauber (1935a) also noted that ground color shifts toward olive-brown and green near the NM border in Apache Co., which he attributed to intergradation with *C. v. viridis*. Similarly, in Coconino Co., west of the core range of typical *nuntius*, snakes are larger and darker, being predominantly brownish (Fig. 7; Klauber 1935a; TBP, pers. obs.). Color can also be affected by temperature, with cooler temperatures evoking dispersion of melanophores and darkening the skin (Rahn 1942a). The dorsal surface is marked with a series of oval to quadrangular, large, brown blotches, usually with thin, white edges and often indented at the front and back, which tend to form crossbands posteriorly (Campbell and Lamar 2004). Dorsal blotches are commonly fused, sometimes forming partial stripes, particularly anteriorly (TBP, pers. obs.). There are two rows of smaller, brown blotches on the sides, the upper ones diffuse and slightly darker than the ground color and the lower ones more pronounced, similar in darkness to the dorsal blotches (Lowe *et al.* 1986). Numbers of dorsal blotches are similar between *C. v. nuntius* in AZ (33-53, \bar{x} = 41.7) and *C. v. viridis* elsewhere (33-57, \bar{x} = 43.7; Klauber 1972). Although Klauber (1972) did not provide sample sizes, similar figures (35-52, \bar{x} = 42.2 \pm 0.23) are given for a sample of 108 typical *C. v. nuntius* from the Little Colorado River Basin (Klauber 1935a). A dark postocular stripe extends from behind the eye to the corner of the mouth and is bordered above and below by thin, light stripes that are 1-2 scale rows wide, and a light-edged dark bar crosses the supraoculars on the top of the head (Klauber

1935a; Campbell and Lamar 2004). The venter is whitish, pale gray, or straw-colored, with little or no dark marking (Klauber 1935a; Campbell and Lamar 2004). Dark tail bands are generally similar in color to the dorsal blotches, although the terminal 1-2 bands may be almost black (Campbell and Lamar 2004). Klauber (1972) reported an albino *C. viridis* from CO, and Thesing and Jech (2018) illustrated a melanistic adult from WY.

SCUTELLATION. Head scales include 2 preoculars, 2 postoculars, and usually a single loreal on each side (Ernst and Ernst 2012). The top of the head has 4-6 intersupraoculars, 2 pairs of canthals, and 7-45 (usually 15-30) small scales in front of the supraoculars (Campbell and Lamar 2004). The rostral scale is usually higher than wide, and usually has more than 2 (mode of 4) internasals in contact with it (Campbell and Lamar 2004). There are 10-18 (mode of 15) supralabials and 11-19 (usually 15 or 16) infralabials (Campbell and Lamar 2004). Dorsal scales are keeled and in 21-29 rows at mid-body (Klauber 1972). In most AZ specimens (*i.e.*, *C. v. nuntius*), these usually number 23 or 25 (mode of 25), whereas elsewhere throughout the range (*i.e.*, *C. v. viridis*) the mode is 27 (Klauber 1935a, 1972). The cloacal scute and most subcaudals are undivided. Ventrals number 164-187 (\bar{x} = 177.4) and 171-196 (\bar{x} = 184.4) in *C. v. viridis* males and females, respectively, and 163-178 (\bar{x} = 171.2) and 169-184 (\bar{x} = 176.6) in *C. v. nuntius* males and females, respectively (Klauber 1972). Subcaudals number 21-31 (\bar{x} = 26.1) and 16-25 (\bar{x} = 20.2) in *C. v. viridis* males and females, respectively, and 21-28 (\bar{x} = 24.9) and 14-22 (\bar{x} = 18.6) in *C. v. nuntius* males and females, respectively (Klauber 1972).

SIMILAR SPECIES. *Crotalus viridis* is most likely to be confused with other members of the *C. viridis* complex. The dorsal blotches of adult *C. oreganus* are not thinly outlined with white as in *C. viridis*, although those of juveniles, especially neonates, often are (*e.g.*, Feldner *et al.* 2016a,b,c). In both

C. cerberus and *C. oreganus*, the light postocular stripe is noticeably wider (2 or more scales wide) than in *C. viridis* (1-2 scale rows wide) and is often indistinct. *Crotalus scutulatus* is superficially similar in both color and pattern to *C. viridis* but can be distinguished by the absence of thin, light borders to the dorsal blotches, the presence of black-and-white bands on the tail, and the presence of two large intersupraocular scales (typically).

DISTRIBUTION AND ABUNDANCE. *Crotalus viridis* primarily inhabits the Great Plains, ranging from southern Alberta and Saskatchewan in Canada south to extreme northern México (Campbell and Lamar 2004). It occurs over most of CO, MT, NM, and WY and the western parts of KS, ND, NE, OK, SD, and TX, with the easternmost outlying records coming from southwestern MN and extreme western IA; in the north, it crosses the Continental Divide in MT into east-central ID, and in the south it extends as far west as southeastern UT and north-central AZ (Campbell and Lamar 2004). *Crotalus viridis* barely extends into México, occurring in northern Chihuahua, Coahuila, and Sonora (Campbell and Lamar 2004). In extreme northeastern Sonora, it is found in grasslands at the southern end of the Animas Valley (Rorabaugh and Lemos Espinal 2016).

In AZ, *C. viridis* occurs above the Mogollon Rim across most of Apache, Coconino, and Navajo counties, south and east of the Colorado River (Map 7). The two westernmost localities, both on the Coconino Plateau, are from *ca.* 16 km east (UAZ 52115) and 29 km north (ASU HP00326; Fig. 11 in Davis and Douglas 2016) of Rose Well, locations farther west than those described by Klauber (1935a). Klauber (1935a) considered most specimens from AZ that he examined to represent *C. v. nuntius* except those from the base of the Echo Cliffs and near Lees Ferry in Coconino Co., from Kayenta and Marsh Pass in northern Navajo Co., and from the San Juan River Basin (Four Corners area) in Apache Co., which he considered to be *C. v. viridis*. Boundy (1992) reported three *C. v. viridis* from the Springerville

area, Apache Co., as the first records of the subspecies from east-central AZ.

QUESTIONABLE LOCALITIES. Klauber (1935a) listed a specimen of *C. v. nuntius* from "Havasupai Point, South Rim, Grand Canyon," which he incorrectly plotted as near the village of Supai, along Havasu Creek, which is *ca.* 31 km west of Havasupai Point. This was presumably GCNP 928, which has been deaccessioned from the Grand Canyon National Park collection and thus was unavailable for study. The specimen may have represented *C. viridis*, although other *C. viridis* complex specimens along the South Rim are *C. o. abyssus* (Map 7), including two from the immediate vicinity of Havasupai Point (ASU HP00145 and GCNP 995). Fowlie (1965) plotted a record of *C. v. nuntius* from 13.6 km east of Kingman, Mohave Co., but this likely represented a *C. cerberus*.

While some sources depict the range of *C. v. viridis* as extending across the NM border into extreme eastern Cochise Co. (*e.g.*, Klauber 1972; Lowe *et al.* 1986; Stebbins 2003), the species had not been vouchered from southeastern AZ as of 2016 (Brennan and Holycross 2006; Davis and Douglas 2016). Douglas *et al.* (2002) list a *C. v. viridis* mtDNA haplotype recovered from "Portal Road, 0.4 km W of New Mexico state line" in Cochise Co., but to our knowledge no voucher specimen was retained. A snake photographed in 2017 in the northern San Bernardino Valley (ASU HP00167) appears to be morphologically consistent with *C. viridis* but might represent a hybrid with *C. scutulatus* (neither a specimen nor tissue was taken). The photograph (Fig. 8) shows only two internasals contact the rostral and only three scales separate the anterior end of the supraoculars. A hybrid zone between these two species has been documented *ca.* 50 km NE of the locality of ASU HP00167 (Zancolli *et al.* 2016).

STATUS AND TRENDS. Although, like most rattlesnakes, *C. viridis* is sometimes subject to human persecution (*e.g.*, Hammerson 1999), it is



FIGURE 3. *Crotalus viridis* (Prairie Rattlesnake) from the vicinity of Holbrook, Navajo Co. Photo by Randall D. Babb.

common over most of its range in AZ. For example, during road-driving surveys at Wupatki National Monument, northeast of Flagstaff, it was the second most frequently encountered snake species ($n = 43$), after *Pituophis catenifer* ($n = 48$; Persons 2001). Similarly, *C. viridis* was the third most common species ($n = 28$) found during nighttime road surveys at Petrified Forest National Park, after *P. catenifer* ($n = 47$) and *Hypsiglena jani* ($n = 33$; Drost *et al.* 2001). Persons *et al.* (2008) documented *C. viridis* from 16 National Park Service units across the southern Colorado Plateau and stated that it probably occurred in all others as well. As noted by Davis and Douglas (2016), there are few museum specimens of *C. viridis* from the western part of the Coconino Plateau (Map 7), but this may be due to lack of collecting effort rather than rarity of the species in the region. *Crotalus viridis* is strongly associated with *Cynomys ludovicianus* (Black-tailed Prairie Dog) towns on the Great Plains (Klauber 1972), and although *Cynomys gunnisoni* (Gunnison's Prairie Dog) generally forms smaller colonies, it is possible that the historical reduction of this species by humans throughout northern AZ (Hoffmeister 1986) has similarly reduced some rattlesnake populations.

■ **HABITAT.** Although primarily a species of open grasslands over much of its extensive range (*e.g.*,



FIGURE 4. *Crotalus viridis* (Prairie Rattlesnake) from south of Winslow, Navajo Co. Photo by Trevor B. Persons.

the Great Plains), *C. viridis* occurs in a variety of biotic communities in AZ, including Great Basin Desertscrub, Plains and Great Basin grasslands, and Great Basin Conifer Woodland. Hammerson (1999) noted that soils in habitats used by *C. viridis* in CO varied from sandy to rocky and that the species only seemed to avoid perennially wet areas and high mountains. In NM, *C. viridis* is most common in remnant grasslands with sandy or alkali soils but also occurs in open desert, rocky hillsides, and overgrazed shortgrass prairie (Degenhardt *et al.* 1996). In WY shrubland habitat dominated by greasewood (*Sarcobatus vermiculatus*) and big sagebrush (*Artemisia tridentata*), Brown and Duvall (1993) observed that *C. viridis* avoided greasewood during its annual shed cycle, possibly due to high salinity levels near these plants causing osmotic problems for the snakes during shedding. In grassland and woodland habitats on the Coconino Plateau, *C. viridis* is often associated with volcanic outcrops (Davis and Douglas 2016; TBP, pers. obs.). At Petrified Forest National Park, typical diminutive *C. v. nuntius* were found in all habitats throughout the park, including grasslands, eroded badlands, riparian areas, and developed housing areas (Drost *et al.* 1999).

The lowest elevation reported in AZ is 1,372 m ASL at Moenkopi Wash, Coconino Co. (USNM 4251), but the species is probably found at least as low as ~1,280 m ASL where Moenkopi Wash



FIGURE 5. *Crotalus viridis* (Prairie Rattlesnake) from south of Winslow, Navajo Co. Photo by William Wells.

meets the Little Colorado River near Cameron, or perhaps lower if it occurs significantly downstream along the Little Colorado River before being replaced by *C. o. abyssus*. The highest elevation reported in the state is 2,591 m ASL from 8 km south of Greer, Apache Co. (USNM 101845). Hammerson (1999) reported an upper elevation limit of 2,895 m ASL in CO.

■ **DIET AND FORAGING BIOLOGY.** *Crotalus viridis* has one of the most varied diets of any North American rattlesnake. It is sometimes considered a specialist on small mammals, and mammals do form the bulk of its diet, but it has also been documented feeding on amphibians, lizards, snakes, birds, eggs, insects, and carrion (Klauber 1972). A population inhabiting a prairie dog town in the Sand Hills of NE primarily preyed on *Dipodomys ordii* (Ord's Kangaroo Rat; Holycross 1993). *Peromyscus maniculatus* (Deer Mouse) was the predominant prey in WY (Duvall *et al.* 1985). In Alberta, Canada, small mammals made up 91% of gut contents, and unidentified passerine birds accounted for 9% (Hill *et al.* 2001). Mammals documented as prey in CO include *Cynomys* spp. (prairie dogs), *D. ordii*, *Perognathus* spp. (pocket mice), *P. maniculatus*, *Reithrodontomys megalotis* (Western Harvest Mouse), *Spermophilus* spp. (*sensu lato*; ground squirrels), *Neotamias* spp. (chipmunks), and *Sylvilagus* spp. (cottontails; Hammerson 1999).



FIGURE 6. *Crotalus viridis* (Prairie Rattlesnake) emerging from a den site in the vicinity of Meteor Crater, Coconino Co., on 29 March 2015. Photo by Bryan Hughes.

In contrast to the primarily mammalian diet of adults, young *C. viridis* often prey on lizards. For example, Klauber (1972) reported that neonates collected in eastern CO regurgitated *Holbrookia maculata* (Common Lesser Earless Lizard) and *Sceloporus consobrinus* (Prairie Lizard), whereas larger snakes regurgitated mice, presumably *Peromyscus*. Conversely, Graves (1991) reported that a 290 mm TL neonate *C. viridis* from WY weighing 15.8 g had eaten a 12.1 g *P. maniculatus*, 77% of the snake's body weight. Larger *C. viridis* also sometimes eat lizards. Hammerson (1999) found a 475 mm TL DOR *C. viridis* in San Juan Co., UT, that contained the tail of an *Aspidoscelis* (whiptail lizard) and an undigested 80 mm SVL *Sceloporus magister* (Desert Spiny Lizard). Hamilton (1950) reported that of seven (presumably adult; no sizes given) *C. viridis* collected in the Black Hills of SD, two contained *Phrynosoma hernandesi* (Greater Short-horned Lizard), in addition to all seven containing *Microtus* sp. (voles). Davis and LaDuc (2011) found a 606 mm TL *C. viridis* in TX that had eaten a 102 mm SVL *Phrynosoma cornutum* (Texas Horned Lizard). Chiszar *et al.* (1993) reported feeding behavior of a juvenile (<1 year old) *C. viridis* in CO in which, after striking and releasing an adult *S. consobrinus*, the snake was observed to discriminate between the pre-enuvenomation and post-enuvenomation trails of the lizard, preferring the latter. Reports of amphibian prey are

few, but one *C. viridis* was seen to have recently envenomated a *Scaphiopus couchii* (Couch's Spadefoot) in TX (Hansen and Bryson 2018), and another unidentified spadefoot (presumably *Spea bombifrons* [Plains Spadefoot] based on location) was identified in stomach contents from a *C. viridis* in CO (Stabler 1948). Birds taken typically include passerines such as *Calamospiza melanocorys* (Lark Bunting; Bateman 1918), *Chondestes grammacus* (Lark Sparrow; Klauber 1972), and *Sturnella neglecta* (Western Meadowlark; Klauber 1972; Gannon and Secoy 1984), but sometimes much larger birds are taken, or at least predation is attempted on them. A *C. viridis* was observed ingesting an adult male *Falco sparverius* (American Kestrel) in NM, but the bird was later regurgitated (Chepsongol and Burkett 2013). Klauber (1972) reported secondhand accounts of attempted predation on a *Corvus* sp. (raven) and a phasianid (grouse).

Cannibalism in *C. viridis* has been documented rarely, and Klauber (1972) questioned whether most instances involved carrion feeding. Beetles of unspecified number and species were reported from *C. viridis* in TX (McKinney and Ballinger 1966), and grasshoppers and *Anabrus simplex* (Mormon Cricket) have been found in stomachs, but it is not known whether these might have been ingested incidentally to other prey (Klauber 1972). Scavenging has also been uncommonly reported. An adult *C. viridis* had ingested the cranial half of a *Cratogeomys castanops* (Yellow-faced Pocket Gopher) in TX (Giovanni *et al.* 2005). The snake was directly below an active *Buteo regalis* (Ferruginous Hawk) nest and apparently scavenged the gopher after it fell from the nest. *Crotalus viridis* has also been reported to scavenge road-killed *Sceloporus clarkii* (Clark's Spiny Lizard) in NM (Gomez and Geluso 2018) and *Ictidomys tridecemlineatus* (Thirteen-lined Ground Squirrel) in ND (Ernst 1992).

There is almost no published data on diet of *C. viridis* in AZ. Roden *et al.* (2020) reported that a *C. viridis* north of Flagstaff had eaten and regurgitated a radio-tagged *Peromyscus truei*

(Pinyon Mouse). While Klauber (1972) only found mammal hair in five specimens of *C. v. nuntius* (presumably from AZ), he speculated that younger individuals likely prey extensively on lizards, especially *H. maculata*.

■ **PREDATORS AND PARASITES.** Known predators include eagles, hawks, coyotes, bobcats, skunks, foxes, and humans (Klauber 1972; Duvall 1986). *Taxidea taxus* (American Badger) commonly preys on rattlesnakes, as Jackley (1938) reported for *C. viridis* inhabiting prairie dog towns in SD. Four juvenile *C. viridis* in WY, three dead and one barely alive, were discovered with *Formica* sp. (ants) consuming them (Graves 1989). Klauber (1972) includes an anecdotal report of a rattlesnake in CO (probably *C. viridis*) attacked and killed by a "flock" (perhaps a family group) of *Dolichonyx oryzivorus* (Bobolink). *Crotalus viridis* has been intentionally or incidentally trampled by deer, pronghorn, horses, goats, and cattle (Klauber 1972). Kingsnakes, particularly *Lampropeltis californiae*, are well known for their habit of preying on rattlesnakes (Klauber 1972). At Wupatki National Monument northeast of Flagstaff, a ~1,067 mm TL *L. californiae* consumed a ~610 mm TL *C. viridis* (complete rattle string of seven segments, including terminal button) between 2015 h and 2240 h on 19 August 1972 (J.K. Walthuis, pers. comm.).

Widmer (1967) examined 204 *C. viridis* from CO and documented three species of helminth parasites, including *Kaliocephalus inermis*, *Rhabdias* sp., and *Physaloptera* sp. The *Physaloptera* sp. was later shown to be *P. rara* (Widmer 1970). *Eimeria cascabeli*, an apicomplexan parasite, was described from *C. viridis* in northern CO (Vetterling and Widmer 1968), and *E. crotalviridis* was described from *C. viridis* in NM (Duszynski *et al.* 1977). A cestode (*Oochoristica osheroffi*) and two nematode species (*K. inermis* and *P. retusa*) were recovered from two infected *C. viridis* in NM (Pfaffenberger *et al.* 1989). In SD, 21% of *C. viridis* were infected with at least one of six helminth parasites, including *Manodistomum* sp.,

Mesocestoides sp., *Physaloptera* sp., two different species of oligacanthorhynchid acanthocephalan, and an unidentified acanthocephalan (Bolette 1998). While the species of *Mesocestoides* was not known, laboratory studies have shown *C. viridis* to be susceptible to at least *M. corti* (Hanson and Widmer 1985). An unidentified argasid (soft tick) was reported from *C. viridis* in Chihuahua, México (Gatica-Colima *et al.* 2014). Ten different bacterial species have been isolated from *C. viridis* oral cavities, six of which have the potential to induce human disease; fecal samples included 13 bacterial species, of which 12 can cause disease in humans (Fitzgerald *et al.* 2013).

A tumor-like lump was extracted from the mouth of a single *C. viridis* in CO (Mackessy 2010a). Two seed heads from spiny burr grass (*Cenchrus longispinus*, an invasive grass found throughout the western United States) were found to be the source of the lump, which may have become embedded while ingesting rodent prey. The long-term effects of swallowing these seed heads are unknown.

■ **BEHAVIOR.** Seasonal activity of *C. viridis* varies across its wide latitudinal range. At the northern edge of its range in Saskatchewan, snakes emerge from hibernacula in late April and migrate away from those areas in early May, then return in early September and remain active near hibernacula until early October (Gannon and Secoy 1985). In the Haystack Mountains of southern WY, the growing season is even shorter than at Gannon and Secoy's (1985) study site in Saskatchewan, with only about 95 frost-free days each summer season, and with egress and ingress of *C. viridis* at hibernacula peaking around 20 May and 20 September, respectively (King and Duvall 1990). Graves and Duvall (1990) found that *Thamnophis elegans* sharing hibernacula with *C. viridis* in WY emerged about a month earlier, a difference they suggested was partly attributable to the lack of spring mating in the *C. viridis* population. In a central NM grassland, *C. viridis* emerged

and dispersed from a communal hibernaculum between 10 and 29 April, and although ingress dates were not given, a few individuals were noted basking in November and December (Jacob and Painter 1980). Movement of snakes within the den, as well as occasional basking on the surface, occurred as long as snake body temperatures remained above ~10 °C (Jacob and Painter 1980). At a more intensively studied nearby hibernaculum (an abandoned mine adit), emergence dates from 1,363 captures over seven years ranged from 3 March to 27 May, with the vast majority of snakes (74%, $n = 1,003$) emerging in April (Painter and Kamees 2017). In a population using a prairie dog town as communal hibernacula in the Sand Hills of NE, *C. viridis* emerged between 5 and 21 April and returned beginning on 13 September, with basking observed as late as 19 October (Holycross 1993). At high-elevation (2,316–2,530 m ASL) hibernacula fringing the San Luis Valley in southern CO, Hahn (1968) recorded the earliest emergence of *C. viridis* on 19 April and the latest observation in the fall was on 14 September.

Large communal hibernacula have not been reported for *C. viridis* in AZ, although seven snakes found on 29 March on a southeast-facing sandstone outcrop in Coconino Co. appeared to be emerging from a communal den (Fig. 6; Davis and Douglas 2016). Five individuals of various ages occupied the same hole and an additional two adult males were found basking in the immediate vicinity (B. Hughes, pers. comm.). Relatively mild winters compared with those at more northerly latitudes may reduce the need for communal denning in much of the AZ range of *C. viridis*. However, sizeable hibernacula may exist at higher elevations, such as in the White Mountains. Yet even in the high-elevation San Luis Valley in CO most dens were small, which Hahn (1968) attributed to an abundance of suitable hibernacula in the area.

Of AZ vouchers shown on Map 7, the earliest collection date is 15 April, from 19.2 km north of Springerville, Apache Co. (UAZ 27881), and the latest date of an unquestionably active



FIGURE 7. *Crotalus viridis* (Prairie Rattlesnake) from Spring Valley, Coconino Co. (ASU HP00402). Photo by Trent R. Adamson.

snake is 5 November, a DOR juvenile from Wupatki National Monument, Coconino Co. (WUPA 16685). A series of three specimens also collected on 5 November, from Sunshine, Coconino Co. (SDNHM 3737–9), and a series of ten specimens collected 18 December from 9.6 km north of Adamana, Apache Co. (SDNHM 4086–95), may have been collected at communal hibernacula. Of 395 vouchered records from AZ, 52% ($n = 205$) were collected during the monsoon months of July and August. Similarly, 74% ($n = 32$) of 43 *C. viridis* observed on roads at Wupatki National Monument in Coconino Co. between May and November were found in July and August (Persons 2001).

Depending upon temperature, *C. viridis* may be primarily crepuscular and nocturnal during hot summer days, or diurnal on mild or overcast days. Activity of adults peaks on dark nights and is reduced on moonlit nights, but the activity of juveniles does not seem to be affected by moonlight (Clarke *et al.* 1996). In CO, *C. viridis* is most active in afternoon and early evening during mild weather in April–May and September–October, with snakes basking during the day (Hammerson 1999). From June through August, most activity in CO occurs at dusk and during the “early hours of darkness,” although snakes are sometimes active throughout the night or even during mid-afternoon on hot days (Hammerson 1999). At Natural Bridges National Monument in southeastern UT, radio-tracked *C. viridis* in pinyon-juniper habitat at

~1,980 m ASL were active during the day during spring but retreated to the cover of rocks or logs at night, and during summer were observed aboveground almost exclusively, usually resting in the shade of rocks or vegetation during the day (TBP, pers. obs.).

Crotalus viridis is well known for its lengthy seasonal migrations in some northern populations, with individuals traveling up to 9 km from hibernacula in WY (King and Duvall 1990), 11 km in southern Saskatchewan (Gardiner *et al.* 2013), and 25 km in southern Alberta (Didiuk 1999). These migrations are often straight-line movements, which has been interpreted as being an efficient search strategy to find patchily distributed small mammal prey (Duvall *et al.* 1985). However, Bauder *et al.* (2015) suggested that rather than being a searching strategy *per se*, these straight-line movements may often simply represent the most direct movement to previously known annual foraging areas. In a review of *C. viridis* telemetry studies, Jørgensen *et al.* (2008) noted that dispersion distances from hibernacula increase with latitude, and they suggested that greater dispersion distances were a function of decreased prey availability and greater numbers of snakes in communal dens at northern latitudes, the latter a result of limited suitable overwintering sites necessitating large, communal hibernacula. Such long-distance migrations are probably not necessary for *C. viridis* in AZ because milder winter temperatures likely result in an abundance of suitable overwintering sites. In addition, prey may be more abundant in most AZ habitats compared with those at more northerly latitudes. Shorter and less straight-line movements exhibited by *C. viridis* in eastern CO compared with populations in WY were likely a result of greater prey availability at the CO site (ShIPLEY *et al.* 2013; Chiszar *et al.* 2014). Similarly, at Natural Bridges National Monument, small mammal prey was relatively abundant and evenly distributed, and *C. viridis* travelled only 1–2 km from hibernacula over the course of the active season (TBP, pers. obs.).

A female *C. viridis* in southern Alberta showed evidence of “map and compass” navigation (*i.e.*, using both location and direction), as over the period of four months she navigated across the South Saskatchewan River multiple times, including once drifting downstream on the river approximately 2 km, after which she was able to reorient and return to her den (Jørgensen and Gates 2007). This navigation does not seem to be related to following conspecific chemical cues, as adult *C. viridis* actively avoid conspecific pheromones in captivity (King *et al.* 1983b).

Home range estimates vary widely depending on how they are calculated, especially when snakes such as those from many northerly populations of *C. viridis* undertake lengthy straight-line migrations between hibernacula and summer foraging areas. For example, in southern Saskatchewan, Gardiner *et al.* (2013) found home ranges of *C. viridis* to be “dumbbell shaped,” with two activity centers (hibernacula and summer foraging areas) connected by narrow migration corridors. For 13 *C. viridis*, mean MCP home ranges were 109.3 ± 47.1 ha, whereas mean 95% fixed kernel density estimates were only 13.9 ± 1.5 ha (Gardiner *et al.* 2013). In contrast, 27 *C. viridis* (21 males and 6 non-pregnant females) inhabiting mountainous terrain in central ID did not migrate as far away from hibernacula areas during the summer (0.69–2.71 km, $\bar{x} = 1.46$), and mean 95% fixed kernels were larger (96.30 ha) than mean MCP home range estimates (44.79 ha; Bauder *et al.* 2015). *Crotalus viridis* inhabiting prairie dog towns in eastern CO had mean MCP home ranges of 0.3–31.4 ha ($n = 10$), 8.1–28 ha ($n = 4$), and 0.2–28 ha ($n = 5$) for males, non-pregnant females, and pregnant females, respectively (ShIPLEY *et al.* 2013). Home ranges of individual snakes overlapped those of other snakes in the same prairie dog colony, but not those of snakes from nearby colonies (ShIPLEY *et al.* 2013). *Crotalus viridis* in Alberta had mean 95% MCP home ranges of 0.09–52.4 ha ($n = 17$, 16 males and 1 female; Andrus 2010). Home ranges of *C. viridis* in AZ have not been studied.

Body temperatures of *C. viridis* have rarely been reported. Brattstrom (1965) reported that a single *C. v. viridis* (locality not given) had a body temperature of 34.1 °C, with corresponding air and soil temperatures of 29.5 °C and 34.0 °C, respectively. In WY, Graves and Duvall (1993) found that the mean active-season body temperature of six pregnant female *C. viridis* was 26.5 ± 0.26 °C, with no observations >36 °C, which they suggested approximated the maximum voluntary body temperature. Their data demonstrated active thermoregulation in that at lower ambient temperatures, body temperatures were generally higher than ambient temperature, whereas at the highest ambient temperatures, body temperatures were generally lower than ambient temperature (Graves and Duvall 1993). Also at their study site, which was relatively exposed and treeless (*e.g.*, Duvall *et al.* 1985), snakes were underground during 65% of observations, especially at lower and higher substrate temperatures (Graves and Duvall 1993). In southeastern UT, mean body temperature of 12 *C. viridis* was 18.4–26.7 °C ($\bar{x} = 22.5 \pm 6.98$), with substrate temperature best predicting body temperature (Graham *et al.* 1995). A pregnant female maintained a higher (~31 °C) and more constant body temperature during her sedentary incubation period from early June to mid-August (Graham *et al.* 1995).

While Klauber (1972) considered the various members of the *C. viridis* complex to be similar in temperament and to represent the “rattlesnake mode,” Lowe *et al.* (1986) stated that *C. v. viridis* (*i.e.*, exclusive of *C. v. nuntius*) was the “most temperamental” member of the complex in AZ. Defensive behaviors are relatively well studied in *C. viridis*. Kissner *et al.* (1997) tested the effects of sex, reproductive status, body size, and body temperature on rattling when approached by an observer. Gravid females allowed significantly closer approach than did males, and smaller snakes allowed significantly closer approach than did larger snakes. They hypothesized that gravid



FIGURE 8. A juvenile snake (ASU HP00167) from the northern San Bernardino Valley, Cochise Co., that is generally morphologically consistent with *Crotalus viridis* (Prairie Rattlesnake), but also shows some scutellation characters that align better with *Crotalus scutulatus* (Mohave Rattlesnake). Photo by J. Clayton Sharp.

females may display a greater reliance on crypsis due to their constrained locomotor abilities, and smaller snakes may be more cryptic than larger snakes, thus allowing a closer approach before rattling (Kissner *et al.* 1997). In addition, gravid females allowed closer approach at lower body temperatures, suggesting a relationship between cryptic behavior and locomotor ability (Kissner *et al.* 1997).

Striking in *C. viridis* is affected by factors similar to those affecting rattling behavior (Duvall *et al.* 1985). Crypsis is typically employed as the first line of defense, especially when sufficient cover is present. Once discovered, individuals attempt to crawl away from the perceived threat. If further intimidated, snakes may coil or stretch out so that the head and upper third of the body are positioned for a bite, and if further disturbed, they strike (Duvall *et al.* 1985). Propensity to strike is increased at colder body temperatures for pregnant females but not for males or non-pregnant females (Goode and Duvall 1989).

Body bridging is a typical response by rattlesnakes to potentially predatory kingsnakes and has been demonstrated in both *C. v. nuntius* (Carpenter and Gillingham 1975) and *C. v. viridis* (Bogert 1941).

■ **REPRODUCTION.** Klauber (1935a) reported that the smallest mature female *C. v. viridis* he examined from CO measured 588 mm TL, and the smallest mature female *C. v. nuntius*, from near Winslow, was 395 mm TL. Ashton (2001), citing Klauber's unpublished data, reported figures presumably from the same samples of 555 and 376 mm SVL, respectively. Aldridge (1979) reported the smallest "adult" female *C. viridis* from NM as 510 mm SVL, but the smallest plotted on his graph of SVL vs. number of eggs is ~545 mm SVL. A female captured at a hibernaculum in NM on 14 November that measured 482 mm SVL and 510 mm TL contained five follicles (Painter and Kamees 2017). Male *C. viridis* >540 mm SVL from NM had completed spermatogenesis (R.D. Aldridge *in* Painter and Kamees 2017).

Spermatogenesis is initiated by warming temperatures in the spring rather than changes in photoperiod (Aldridge 1975). Spermatogenesis peaks in July and August, but sperm are present in the *vas deferens* all year (Aldridge 1993). Like other rattlesnakes, in female *C. viridis* vitellogenesis begins in summer or early fall, pauses during hibernation, and resumes the following spring (Aldridge 1979a; Aldridge and Duvall 2002). Mating occurs exclusively, or almost exclusively, in mid- to late summer, usually in July and August (*e.g.*, King and Duvall 1990; Schuett *et al.* 1993; Aldridge and Duvall 2002). Thus, long-term sperm storage by females is obligatory (Schuett 1992), and females store sperm in the oviduct over the winter for fertilization in the spring (Ludwig and Rahn 1943). Holycross (1995) reported a single courtship event on 6 April in NE, but neither copulation nor eversion of the male's hemipenes was observed. Both snakes had recently shed (the positively identified sloughed skins were found nearby), supporting the hypothesis that release of pheromones from the skin during ecdysis signals female receptivity (Holycross 1995; Duvall *et al.* 1992). Males typically do not pursue prey during the mating season (July and August), but females continue to feed throughout the entire active season (King and Duvall 1990).

As in other pitvipers, male combat behavior in *C. viridis* is a typical component of reproduction (Aldridge and Duvall 2002). Although it is usually observed during the summer mating season (*e.g.*, Klauber 1972; Aldridge 1993; Holycross 1995), Gloyd (1947) described typical male combat in *C. viridis* on 20 April in MT. Gloyd (1947), as others before him, interpreted the observation as courtship, but Lowe (1948b) first recognized it as male-male combat. Dawson and Mackessy (2018) reported the first known instance of three male rattlesnakes in combat, all of which were *C. viridis* from CO. This episode was documented by time-lapse photography at the entrance to a large hibernaculum on 14 April, and because spring mating was never observed in over 15 years of observation at this den, the combat was likely dominance display unrelated to courtship (Dawson and Mackessy 2018). Male combat is apparently sometimes prompted by the presence of a nearby female that is either pregnant or has recently given birth. Cage (2004) observed *C. viridis* male combat in NM "at the end of this summer" that took place near a pregnant female nearing ecdysis, which may have thus released pheromones prompting the combat behavior. In northern Chihuahua, Macias-Rodriguez *et al.* (2013) observed combat by two male *C. viridis* about 20 m away from a female and her newborn young on 23 September, after the typical summer mating season. Macias-Rodriguez *et al.* (2013) also reported male combat from northern Chihuahua in spring (15 April) but did not note whether any female *C. viridis* were present.

Although males combat for females, mate searching ability may be a more important determinant of reproductive success than combat, as fewer than half of males find a female during the breeding season (Duvall and Schuett 1997). Males that do find females sometimes accompany them for long periods (Duvall *et al.* 1985). Courtship typically involves forward jerking with chin rubbing, tail searching, and then a stationary period, with this cycle repeated many times before intromission (Hayes *et al.* 1992).

Courtship can last 2–4 days (Duvall *et al.* 1993). Duvall *et al.* (1985) described copulation in WY that lasted for 90 minutes.

Gestation lasts approximately one year, with parturition typically occurring in late summer and fall of the year following mating (*e.g.*, Duvall *et al.* 1985). In WY, 6–14 pregnant female *C. viridis* inhabited a rookery near the hibernaculum during the summer months and remained there until parturition (Duvall *et al.* 1985; Graves *et al.* 1986; Graves and Duvall 1993). This rookery was characterized by large, flat table rocks with abandoned mammal burrows beneath them (Duvall *et al.* 1985). Pregnant snakes spend much of their time at rookeries basking, and daily movements are associated primarily with thermoregulation (Graves and Duvall 1993). In one year, several of the females at this rookery gave birth between 2 and 12 September (Duvall *et al.* 1985). In southeastern UT, a pregnant female *C. viridis* migrated approximately 325 m from her den in spring and then remained in a 30 m² area for 79 days until giving birth on 10 August (Graham *et al.* 1995). During this time, she remained near a sandstone outcrop on the rim of a small canyon and was usually found basking under the edge of a small rock overhang (TBP, pers. obs.). No communal rookeries were found in this population, possibly because suitable rocky habitat was abundant (Graham *et al.* 1995). An abundance of suitable rookery sites in much of the range of *C. viridis* in AZ, as well as a warmer climate compared with WY, might be expected to limit the use of communal rookeries in AZ.

Larger females reproduce more frequently and contain more follicles than smaller females (Aldridge 1979a; Graves and Duvall 1993). Clutch size based on enlarged follicles or oviductal eggs in female *C. viridis* from NM was 5–14 ($\bar{x} = 9.5 \pm 0.6$ SE, $n = 23$; Aldridge 1979a). Clutch size of *C. v. viridis* from WY and northeastern CO was 4–21 ($\bar{x} = 11.4$, $n = 307$) and clutch size of *C. v. nuntius* from AZ was 3–10 ($\bar{x} = 7$, $n = 10$; Klauber 1972). The female from southeastern UT (above) gave birth to six young (TBP, pers. obs.).

Stillborn young and infertile eggs are common in rattlesnakes, including in this species: in KS, 12.2% of ova failed to develop due to infertility or fetal death (Fitch 1985a). The smallest *C. v. viridis* measured by Klauber (1972) was 212 mm TL, and he estimated the average size at birth to be 270 mm TL; although the smallest *C. v. nuntius* he measured was 233 mm TL, he suggested that the average size at birth was 180 mm TL, indicating he did not have any newborn young in his sample. Neonate *C. viridis* in NE feed prior to their first hibernation (Holycross and Fawcett 2002), apparently in contrast to other rattlesnakes at northern latitudes (*e.g.*, Macartney 1989; Wallace and Diller 1990).

There is typically a short period of maternal care, with the female often remaining with young until their first ecdysis as much as 14 days after birth (Greene *et al.* 2002). Two adult *C. viridis* were observed with young in SD, one with six young within a *Cynomys ludovicianus* burrow, and the other with 4–6 young in a bed of prickly pear cactus (*Opuntia* sp.; Cunningham *et al.* 1996). In WY, neonates remained as clumped aggregations for about 10 days after birth, with mothers staying in attendance for “at least a few days” (Duvall *et al.* 1985). In NE, two adult females were found with 31 neonates, which suggests that not only do females remain with newborn young, but also that females may sometimes aggregate to give birth (Holycross and Fawcett 2002). The female *C. viridis* from southeastern UT (above) left her birth site after two days of attendance, and the six young remained until shedding 9–10 days after birth (TBP, pers obs.; Greene *et al.* 2002). Aggregation of neonates until their first shed limits cutaneous water loss, and maternal attendance probably helps neonates follow scent trails to hibernacula (Graves *et al.* 1986).

Over most of its range, *C. viridis* probably reproduces biennially, although there is variation between localities and between years at a given locality. In southeastern WY, Rahn (1942b) found that of 47 adult females collected at dens in fall and winter, 27 (57%)

were “ripe” based on large developing follicles and presence of motile sperm, and 20 (43%) were recently postpartum. In KS, 70% of females ($n = 20$) had enlarged ova and would likely have produced young that year (Fitch 1985a). In another study, Fitch (1998) concluded that about 80% of mature females captured at the Sharon Springs, KS, rattlesnake roundup produced young each year. Similarly, in NM 73% of females ($n = 44$) showed signs of producing young during the year they were collected (Aldridge 1979a). However, at a high-elevation site in NM, Painter and Kamees (2017) reported that only 35% of females >480 mm SVL ($n = 638$) captured over eight years contained developing follicles. While percentages significantly greater than 50% might seem to suggest that many females reproduce annually, it is possible that they simply represent a “snapshot” of a good year for reproduction, possibly coming on the heels of one or more bad years (*e.g.*, of decreased prey availability) when fewer snakes could acquire sufficient fat reserves to produce young. Fifty-eight percent ($n = 57$) and 50% ($n = 40$) of female *C. viridis* were pregnant in successive years in southern Saskatchewan (Gannon and Secoy 1984). The percentage of female *C. viridis* breeding varied significantly over five years in WY, ranging from 17 to 63% ($\bar{x} = 34\%$, $n = 157$; Graves and Duvall 1993). Estimates of reproductive periodicity based on samples of pregnant vs. non-pregnant females can be misleading. For example, Brown (1991) found that about half of all mature female *Crotalus horridus* (Timber Rattlesnake) captured over all years of his study were pregnant, but mark-recapture data on individual snakes showed that most females had triennial cycles. Such discrepancies may be due to differential behavior (*e.g.*, conspicuous basking at rookeries) that results in pregnant females being more likely to be captured by researchers. Flexibility in reproductive cycles allows females to concentrate on foraging some years and reproduction other years, depending on weather, prey availability, and individual fat

stores (Graves and Duvall 1993). The reproductive cycle of *C. viridis* in AZ is unknown, but a biennial cycle would not be surprising.

■ **REMARKS.** Bailey *et al.* (1989) reported on a *C. viridis* from KS that in 1988 had been maintained in captivity for 27 y, 9 m, and was about 2 years old at the time of capture; it died a year later, at about 31 years of age (Collins 1989). This is in contrast to the estimate made by Fitch (1985a) that few *C. viridis* live to be more than eight years old in the wild. Hybridization was reported between *Crotalus scutulatus* and *C. viridis* in TX (Murphy and Crabtree 1988). Hybridization between these two species was inferred on the basis of venom characteristics in southwestern NM by Glenn and Straight (1990), although the snakes in question appeared typical for *C. viridis* and did not present any visual characters of *C. scutulatus*. More recently, Zancolli *et al.* (2016) identified a narrow hybrid zone just to the east of AZ in the northern Animas Valley, Hidalgo Co., NM, in which hybridization between *C. viridis* and *C. scutulatus* was detected through analysis of morphology, mitochondrial and nuclear DNA, and venom components (Mojave toxin).

Klauber (1972) reported average venom yields (dry weight) of 44 mg (maximum 162) for *C. v. viridis* and 51 mg (maximum 72) for *C. v. nuntius*. Not surprisingly, venom yields vary dramatically with snake body size. In *C. viridis* from SD and CO, venom yields averaged 4.6–6.2 mg for snakes ~300 mm TL and 80–101 mg for snakes ~1,000 mm TL (Klauber 1972). Mackessy (2010b) examined venom components and lethal toxicity of all members of the *C. viridis* complex. *Crotalus viridis* has moderately toxic venom, with LD₅₀ values (in laboratory mice) of 1.33 mg/kg for *C. v. nuntius* and 1.55 mg/kg for *C. v. viridis* (Mackessy 2010b). These LD₅₀ values are about four times less toxic than that of the most toxic member of the complex, *C. o. concolor* (0.36 mg/kg), but are somewhat more toxic than those of all other members of the complex, including

the AZ representatives *C. o. abyssus* (2.05 mg/kg), *C. o. lutosus* (2.88 mg/kg), and *C. cerberus* (5.40 mg/kg; Mackessy 2010b). Mackessy (2010b) noted that less toxic venoms generally have high levels of metalloproteinase activity (Type I venom), which aids in “predigestion” of slow-dying prey, whereas more toxic venoms generally have low levels of metalloproteinase activity (Type II venom; see the *C. cerberus* and *C. oreganus* accounts for more discussion). Although this dichotomy is highlighted by *C. cerberus* and *C. o. concolor*, which are the least toxic and most toxic members of the *C. viridis* complex, respectively, both *C. v. viridis* and *C. v. nuntius*, with moderately toxic venom, show relatively high levels of metalloproteinase activity (Mackessy 2010b).

Human envenomation by *C. viridis* in AZ is probably rare. All nine rattlesnake-bite fatalities in the state between 1969 and 1984 were presumably from bites by *Crotalus atrox* or *C. scutulatus* (Hardy 1986). Straight and Glenn (1993) reported two fatalities in UT between 1900 and 1990 attributed to *C. viridis*, one of which was a 10-year-old girl who was bitten in northeastern AZ but died in UT.

Taxonomic synopses are presented in Gloyd (1940) and Klauber (1972), and the species has been reviewed by Ernst and Ernst (2003; as *C. viridis* [*sensu lato*]), Campbell and Lamar (2004), Ernst and Ernst (2012), and Davis and Douglas (2016).

■ **ACKNOWLEDGMENTS.** We thank Mark Davis, Andrew Didiuk, Mike Douglas, Martin Feldner, Steven Goldberg, Brent Graves, William Hayes, Gordon Schuett, and Caryn Vaughn for their personal observations, assistance in acquiring literature, and helpful discussions. We thank Flagstaff Area National Monuments staff for access to Joanne Walthuis’ unpublished account of kingsnake predation. Numerous museum staff graciously facilitated our requests for photos or information on specimens in their care. Martin Feldner, Robert Hansen, Jesse Meik, and Brendan O’Connor reviewed the account.