In captivity, a wild-caught adult *C. cerberus* lived for 12 y, 5 m, and 4 d (Snider and Bowler 1992). A second individual captured when likely a yearling has lived for 14 y and 8 m (M.J. Feldner, pers. comm.).

The taxonomy of this species has long been in flux, but emerging details of individuals' capacity for complex color change, habitat use, ecology, and behavior are quite different from those of closely related taxa and provide support for species elevation. Although populations of this recently recognized species are currently stable, potential synergisms between climate change, forest and riparian habitat loss, and emerging zoonotics, combined with a relatively small and disjunct distribution, may severely affect the survival and distribution of future populations. Given these looming potential threats, this now-common species could benefit from proactive conservation planning by state, federal, and private organizations (Nowak and Greene 2016).

Klauber (1972) listed an average dried venom yield for *C. cerberus* of 112 mg and a maximum of 150 mg. *Crotalus cerberus* venom is not especially toxic (as measured by LD$_{50}$ for adult laboratory mice; 6.0 mg/kg) compared to other taxa in the "western rattlesnake group" (see Davis *et al.* 2016b) or compared to *C. oreganus* (3.2 mg/kg; Ernst and Ernst 2012). Mackessy (2010b) reviewed the venom components and toxicity for adults in this species complex, including *C. cerberus*. Of these, adult *C. cerberus* venom was least toxic, and *C. o. concolor* venom was the most toxic, representing a 15-fold difference in toxicity between the two species. *Crotalus cerberus* had very low levels of three serine proteases (involved in the disruption of prey hemostasis) and did not have the abundant small myotoxins that are characteristic of *C. o. concolor* venom (Mackessy *et al.* 2003; Mackessy 2010b). *Crotalus cerberus* venom had by far the highest levels of metalloproteinase activity (involved in prey pre-digestion through hemorrhage and tissue degradation) among the species examined (Mackessy 2010b). This pattern of less toxic venom with higher metalloproteinase activity (*i.e.*, Type I venom) may be explained phylogenetically in *C. cerberus*; it appears to be a basal trait in the western clade (Mackessy 2010b). Conversely, Type II venom, exhibited by *C. o. concolor* (Feldner *et al.* 2016b), has high toxicity and very low metalloproteinase activity.

There appears to be a trade-off between highly toxic venoms (which kill prey quickly) and efficient pre-digestion of prey maximized by the suffusion of venom in tissues, but this process is inhibited in prey that die quickly, potentially limiting the prey size available to species which have Type II venom (Mackessy 2010b). Not surprisingly, *C. cerberus* consumes prey species of varying sizes, from small mice (*P. eremicus*, ~22 g adult mass, Gila Co.) to squirrels (*A. harrisii*, ~100 g, Gila Co.). The ability of *C. cerberus* to effectively consume a range of prey sizes appears to be linked in part to Type I venom properties (Mackessy *et al.* 2003). Some evidence suggests that venom-induced predigestion of prey may be enhanced at cooler ambient temperatures (Thomas and Pough 1979; but see McCue 2007); possessing Type I venom would be adaptive for a rattlesnake occupying higher-elevation, cooler climates.

ACKNOWLEDGMENTS. Novel data presented here were collected by the authors at their respective field sites in Coconino and Gila counties (EMN) and in Cochise (Galiuro Mountains) and Yavapai counties (MA and JJS). This species account could not have been written without the data, support, and abounding enthusiasm for Arizona Black Rattlesnakes provided by J. Schofer, our ghost co-author. We thank the numerous persons and organizations that assisted with the field research on which this account is based. We are indebted to B. Ashley, J. Borgmeyer, T. Brennan, S. Cole, T. Dunn, T. Giermakowski, J. Gillette, A. Holycross, K. Nishikawa, B. O'Connor, R. Paull, D. Prival, J. Purcell, M. Wall, and others for sharing specimen localities and/or unpublished data. Reviews that improved the manuscript were provided by M. Cardwell, M. Feldner, T. Persons, and J. Schofer.

Crotalus lepidus

Rock Rattlesnake

Andrew T. Holycross and Lawrence L.C. Jones

FIGURE 1. *Crotalus lepidus* (Rock Rattlesnake) from the Huachuca Mountains, Cochise Co. Photo by Trent R. Adamson.

TAXONOMY. *Caudisona lepida* was described by Robert Kennicott based on the heads of two rattlesnakes collected from "Presidio del Norte and Eagle Pass that show such remarkable features as to render it justifiable to describe the species from these alone" (Kennicott 1861). Interestingly, Cope was the first to use this name in print, when he included "*Caudisona lepida*" (with a reference to Kennicott's manuscript) in an appendix to Mitchell's (1860) treatise on rattlesnake venom. Neither the collector nor the collection date is stated in Kennicott's (1861) description, and the syntypes were lost not long after their description (Stejneger 1895). Cope (1867b) listed both syntypes as collected from "Rio Grande, Texas" and (based on his observation that the nasals in both specimens were entire) placed them in a new genus, *Aploaspis* (spelling corrected to *Haploaspis* in Cope 1883b). The first complete specimen (KU 2331) was collected by Professor Frank Snow in 1881 from the summit of the Magdalena Mountains (Socorro Co., NM). Cope (1883b) examined and described this specimen and, based on the fact that the nasal was divided below the naris, placed the species in *Crotalus*. Although Garman (1887) described *Crotalus palmeri* and stated it was "closely allied to *C. tigris*," Gloyd (1936b) regarded it as a synonym of *C. lepidus*. Likewise, Tanner *et al.* (1972) regarded Taylor's (1944) *Crotalus semicornutus* as a pattern variant of *C. l. klauberi*, a position reaffirmed by Tanner (1985).

Smith and Taylor (1950) incorrectly restricted the collection locality to Presidio (del Norte), Presidio Co., TX. The historical settlement of Presidio del Norte is actually slightly to the east, in Chihuahua, México. Both Presidio del Norte and Eagle Pass were frontier outposts along the Rio Grande. Eagle Pass, Maverick Co., TX, lies east of the Trans-Pecos and well south of the Edwards Plateau habitats occupied by *C. lepidus* in TX; it is an atypical habitat for the species, one from which no other *C. lepidus* has been collected (T.J. Hibbitts, pers. comm.). The syntypes may have been collected in association with the United States–Mexican boundary survey, which was traveling up and down the Rio Grande in the late 1850s. Kennicott's assignment of one of the missing syntypes' collection locality to Eagle Pass is likely erroneous and might instead represent a shipping locality.

Crotalus lepidus historically contained four subspecies (Campbell and Lamar 2004). Recent molecular phylogenetic studies suggest *C. l. morulus* (Tamaulipan Rock Rattlesnake; Klauber 1952b) should be recognized as a full species (Bryson *et al.* 2014; Blair *et al.* 2018). Of the three remaining subspecies, only *C. l. klauberi* (Banded Rock Rattlesnake; Gloyd 1936b) is found in AZ. The type specimen (UMMZ 79895) is an adult male collected in Carr Canyon, Huachuca Mountains, Cochise Co., by L.H. Cook on 10 August 1930. The two remaining subspecies are *C. l. lepidus* (Mottled Rock Rattlesnake; Kennicott 1861) and *C. l. maculosus* (Durango Rock Rattlesnake; Tanner *et al.* 1972).

The evolutionary relationships of rattlesnakes in the *Crotalus triseriatus* group have been the focus of several recent studies. The earliest one found patterns of genetic structuring consistent with the rugged geography of México and evidence of rangewide undocumented diversity

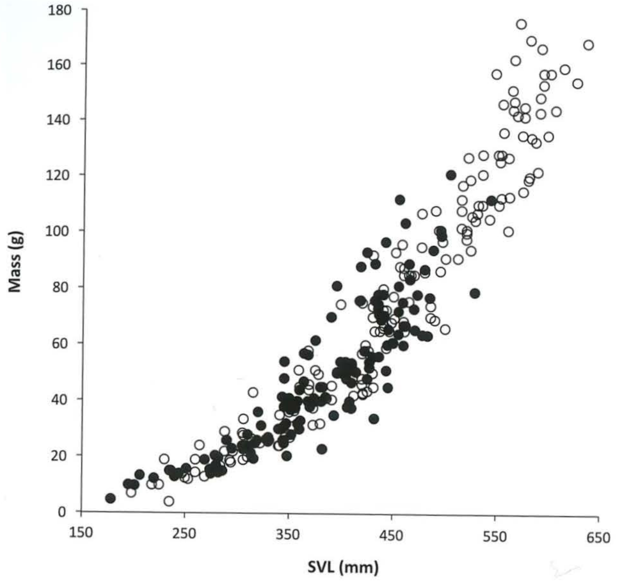

FIGURE 2. Body mass relative to SVL for 169 male (○) and 135 female (●) *Crotalus lepidus klauberi* (Banded Rock Rattlesnake) sampled from the Animas (Hidalgo Co., NM), Chiricahua (Cochise Co., AZ), and Peloncillo (Cochise Co., AZ and Hidalgo Co., NM) mountains. Data collected by ATH and colleagues from 1994 to 2016.

within the group (Bryson *et al.* 2011a). Bryson *et al.* (2014) subsequently used seven nuclear DNA loci to evaluate phylogenetic relationships within the group and inferred nine species, two of which represented new species (*C. campbelli* and *C. tlaloci*). Most recently, Blair *et al.* (2018) used thousands of genes (ultraconserved elements) to infer the phylogeny of the *C. triseriatus* group. In all of these studies, *C. aquilus*, *C. lepidus*, and *C. morulus* form a subclade within the *C. triseriatus* group. *Crotalus lepidus* comprises at least five geographic groups (Bryson *et al.* 2011b; Blair *et al.* 2018), some of which (*e.g.*, *C. l. lepidus* and *C. l. maculosus*) may be morphologically distinct (Dorcas 1992; Campbell and Lamar 2004). *Crotalus l. klauberi* appears to be genetically subdivided across its distribution, with geographic groups corresponding to distinct regions of the Sierra Madre Occidental (Bryson *et al.* 2011a; Blair *et al.* 2018). In the northern part of its range, Dominguez (2000) found little support for infraspecific distinction of *C. l. lepidus* and *C. l. klauberi*, based on morphometric and meristic characters.

ETYMOLOGY. The generic name *Crotalus* (Gr. *krotalon*, or L. *crotalum*, a clapper or castanet) refers to the rattle. The specific name *lepidus* (L. for "pleasant or charming") is presumably a reference to coloration and pattern. The name *klauberi* is a patronym honoring Laurence M. Klauber.

■ DESCRIPTION.

Like other rattlesnakes, *C. lepidus* is relatively heavy-bodied and has vertical pupils, a pair of heat-sensing pits, and a tail terminating in rattles. However, in comparison with other rattlesnakes, *C. lepidus* is relatively thin and small. Adults are from *ca.* 340 to 840 mm TL (Goldberg 2000c; Brennan and Holycross 2006), although Lowe *et al.* (1986) stated that adults are typically 508–610 mm TL. Klauber (1972) reported minimum and maximum sizes of 166 and 828 mm TL. Compared with those of other rattlesnakes, the head is small relative to the body (Fig. 1; Lowe *et al.* 1986), but not to the degree of *Crotalus tigris*, *C. pricei*, or *Sistrurus tergeminus*.

One of us (ATH) recorded SVL and mass of 304 *C. l. klauberi* of all age classes captured in the Animas (Hidalgo Co., NM), Chiricahua (Cochise Co.), and Peloncillo (Cochise Co., AZ, and Hidalgo Co., NM) mountains from 1994 to 2016 (Fig. 2). In this sample, adult males (≥ 352 mm SVL) measured 353–724 mm SVL ($\bar{x} = 489.6 \pm 75.5$, $n = 134$), and adult females (≥ 332 mm SVL) measured 340–543 mm SVL ($\bar{x} = 414.0 \pm 48.2$, $n = 104$). Tails of adult males measured 32–61 mm ($\bar{x} = 44.9 \pm 7.2$, $n = 130$), and adult female tails measured 17–49 mm ($\bar{x} = 30.0 \pm 4.9$, $n = 103$). Tails of adult males were 7.8–10.7% of SVL ($\bar{x} = 9.2 \pm 0.6$, $n = 130$), and adult females' tails were 4.7–9.0% of SVL ($\bar{x} = 7.2 \pm 0.8$, $n = 117$). Adult male mass was 31–179 g ($\bar{x} = 94.1 \pm 38.8$, $n = 133$), and adult female mass was 21–139 g ($\bar{x} = 59.5 \pm 24.2$, $n = 104$). Prival (2008) measured all non-neonate *C. lepidus* he captured in the Chiricahua Mountains and found that males measured 214–541 mm SVL ($\bar{x} = 383.7 \pm 10.2$, $n = 53$), and females measured 207–441 mm SVL ($\bar{x} = 344.7 \pm 8.7$, $n = 48$). Tails of males measured 17.1–50.2 mm ($\bar{x} = 35.4 \pm 1.0$ [misreported as 10.0 in the original publication; D.B. Prival, pers. comm.], $n = 53$), and female tails measured 17.1–34.2 mm ($\bar{x} = 25.2 \pm 0.6$, $n = 48$). In both studies, *C. l. klauberi* exhibited sexual size dimorphism, with males attaining a larger size than females, and females having proportionately shorter tails than males. Neonates averaged about 190 mm TL, but *C. l. klauberi* may be as small as 160 mm TL at birth (Klauber 1972). Six neonates (three of each sex) born to two pairs of captive parents from NM measured 193–240 mm TL and weighed 6–8 g (Swinford 1990).

FIGURE 3. This *Crotalus lepidus* (Rock Rattlesnake) from the Huachuca Mountains, Cochise Co., has distinctive, narrow dark bands and limited mottling between bands; however, *C. lepidus* in AZ exhibit substantial variation in color pattern (see Figs. 4–8). Photo by Bryan Hughes.

Fang length measured 3.2–3.6 mm ($\bar{x} = 3.1$) in a sample of five specimens measuring 520–595 mm TL (Klauber 1939c). Mean number of segments in the rattle chain of museum specimens examined by Rowe *et al.* (2002) was 6.9, whereas individuals examined in the field averaged 6.8 segments (Holycross *in* Rowe *et al.* 2002). In a larger sample from the Animas, Chiricahua, and Peloncillo mountains that only included adults, males had 3–12 rattles ($\bar{x} = 6.0 \pm 1.6$, $n = 118$), and females had 0–9 rattles ($\bar{x} = 5.8 \pm 1.7$, $n = 91$). Christman *et al.* (2004) reported a deformity that resulted in absence of the rattle string, which corresponds to the zero in the preceding data. The hemipenis is short, bifurcate, and has cylindrical to bulbous lobes with 30–54 (usually 36–44) basal spines and 19–26 (usually 22–25) fringes per lobe. It lacks spines at the intersection of the lobes (Klauber 1972; Dorcas 1992).

COLORATION AND PATTERN. Although *C. l. klauberi* was once referred to as the "Green Rock Rattlesnake" (Gloyd 1940; Woodin 1953), there is considerable variation in color and pattern among populations, sexes, and individuals (Figs. 3–7). Ground coloration is gray overall in tone, although this is often suffused to varying degrees with hues

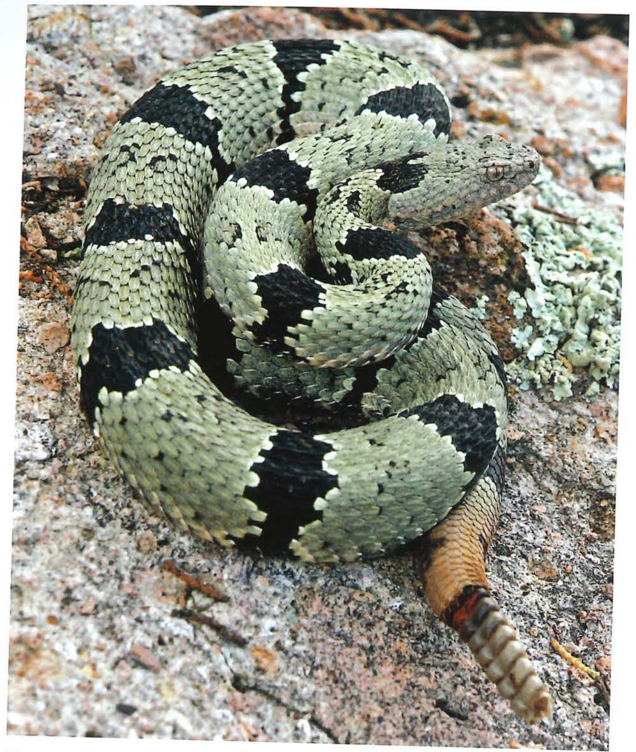

FIGURE 4. *Crotalus lepidus* (Rock Rattlesnake) from the Peloncillo Mountains, Cochise Co. The greenish hue suggests this is an adult male. Photo by Kenny Sharrocks.

of green, blue, tan, brown, red, or lavender; in some individuals, ground coloration is a light pearl-gray (Klauber 1972; Vincent 1982a,b; Prival 2008). In northern (U.S.) populations of *C. l. klauberi*, 13–24 widely separated chestnut-brown to black "bands" contrast remarkably with ground coloration, producing a stunning appearance (Klauber 1972). These bands do not completely encircle the body but typically terminate at or near the lateral edges of the ventral scutes and are sometimes faded or absent on the sides of the body. The serrated edges of the bands are often, but not always, emarginated with flecks or lines of white. In most AZ individuals, the spaces between the dark bands have flecks of darker coloration, although in the Peloncillo Mountains (and populations of *C. l. klauberi* farther east), inter-band flecking can be reduced to absent in some individuals (Figs. 3 and 4). Although the amount of flecking between the bands is highly variable, *C. l. klauberi* tends to have less than *C. l. lepidus* and thus usually does not have an overall appearance of being mottled, particularly in adults. Juveniles sometimes have more inter-band dark pigmentation. The venter of *C. l. klauberi* varies in color, from a dappled gray on cinnamon to a pinkish hue that becomes darker toward the tail (Lowe *et al.* 1986) but tends to be paler overall than in other subspecies (Campbell and Lamar 2004). The head of adult *C. l. klauberi* usually lacks the dark stripe extending from the eye to the posterior supralabials (found to varying degrees in other subspecies), and if present, it is usually faint (Gloyd 1936b). In most *C. lepidus*, a pair of dark occipital blotches matching the color of the dark crossbands is found on the nape of the neck and posterior dorsum of the head. However, in *C. l. klauberi*, these are almost always fused and form a single, butterfly-shaped blotch (Campbell and Lamar 2004). Gloyd (1936b), Klauber (1952b), and Dorcas (1992) regarded the absence of an eye stripe and a single (rather than divided) nuchal blotch as diagnostic of *C. l. klauberi*, although these traits appear to be variable within populations allocated to this subspecies (Dominguez 2000). The tail is usually weakly banded with alternating light ground color and darker rings, although in some individuals, the dorsal bands become increasingly diffuse as they approach the rattle. Neonate *C. l. klauberi* have a yellowish tail (Fig. 8) that transitions to an orangey-salmon in juveniles (Neill 1960). Tail color eventually fades to the adult pattern, although it is still detectable in some young adults (Figs. 3 and 4; Starrett and Holycross 2000).

Several authors have noted sexual dichromatism in *C. l. klauberi*, a trait purported to be absent in other subspecies (Jacob and Altenbach 1977; Van Devender and Lowe 1977; Armstrong and Murphy 1979; Prival 2008; Prival and Porter 2016). In AZ, adult males often have a greenish hue to their background color (Fig. 4; Kauffeld 1943a; Jacob and Altenbach 1977) or a greenish stripe down the back (Fig. 7) and less dark flecking between the dark bands (Gloyd 1936b). Green coloration appears to be associated with onset of sexual maturity, based on Prival's (2008) observation that males under 284 mm SVL "exhibited little or no green." Swinford (1990) also noted that sexual dichromatism was limited to absent in neonates from some southwestern NM mountain ranges. Females are gray or slate gray and sometimes infused with blue or lavender (Fig. 5), although after many years in captivity, some females reportedly develop a greenish hue (H. McCrystal *in* Prival 2008). Prival (2008) suggested this dichromatism is an adaptation for crypsis that corresponds to differences in habitat use by the sexes and differences in habitat use by reproductive condition of females (see "Habitat"). Not all populations of *C. l. klauberi* exhibit sexual dichromatism, as males in the Franklin Mountains of extreme west TX reportedly "exhibit little or no green" (H. McCrystal in Prival 2008).

FIGURE 5. *Crotalus lepidus* (Rock Rattlesnake) from the Huachuca Mountains, Cochise Co. Photo by Richard Legere.

Rangewide, *C. lepidus* has 13–38 narrow and serrate-margined dark bands or blotches, depending on subspecies and populations (Campbell and Lamar 2004). Among the two subspecies extralimital to AZ, a more distinct eye stripe is common, but other aspects of color and pattern are highly variable. The dark crossbands may not reach the venter in some cases, and instead form dorsal blotches. The amount and pattern of pigmentation between the dark bands/blotches is highly variable, as is the boldness of the dark crossbands/blotches, which in some populations are quite faint. The highly variable coloration of *C. l. lepidus* is a polychromatic background color-matching trait (Vincent 1982a,b; Farallo and Forstner 2012). In east TX, animals tend to be lighter in coloration and match the light-colored limestone substrate, whereas those in west TX tend to be darker to match the darker substrates (Farallo and Forstner 2012). Individuals that contrast with the background are more prone to avian attack, supporting a hypothesis of selection for crypsis. To appreciate the full breadth of color patterns of *C. lepidus*, refer to the photograph-rich publications of Price (2009) for the United States and Price (2014) for México, which combined cover most of the species' geographic range. Campbell *et al.* (1989) described pattern, coloration, squamation, and microdermatoglyphics of a preserved natural hybrid of *C. l. klauberi* × *C. willardi obscurus* from the Peloncillo Mountains, Hidalgo Co., NM. On 17 May 2009, Michael Malawy found a rattlesnake that appears to be a natural hybrid between *C. l. klauberi* and *C. w. willardi* in the Santa Rita Mountains, Santa Cruz Co. (Fig. 9).

SCUTELLATION. Dorsal head scales include a rostral that is broader than tall, 2 supraoculars, 1–4 (usually 2) intersupraoculars, 2 large internasals that touch medially and contact the prefrontal area, 5–15 scales in the internasal-prefrontal area, and 1 pair (sometimes 2 pairs) of canthals. Prefrontals are absent. The lateral head scales include 10–15 (usually 12 or 13) supralabials, 9–13 (usually 11 or 12) infralabials, 2–4 (usually 2 or 3) preoculars, 1–5 (usually 2) postoculars, 2–5 (usually 3) suboculars, 0–2 (usually 1) interoculabials, a prenasal that contacts a supralabial, a postnasal (which is usually joined to the prenasal above the nostril), 1 (sometimes 2) loreal(s), and 0–7 (usually 3) small prefoveals. The upper preocular is vertically divided in most individuals, and the anterior portion curves onto the dorsum anterior of the supraocular.

On the chin is a small, broad mental scale and both anterior and posterior pairs of chin shields, with the posterior pair larger. Scale characters and counts are from Campbell and Lamar (2004) and Ernst and Ernst (2012), and may include data from *C. morulus* (Tamaulipan Rock Rattlesnake).

Dorsal scales are keeled and pitted in 21–30 (usually 23–25) anterior dorsal rows, 20–25

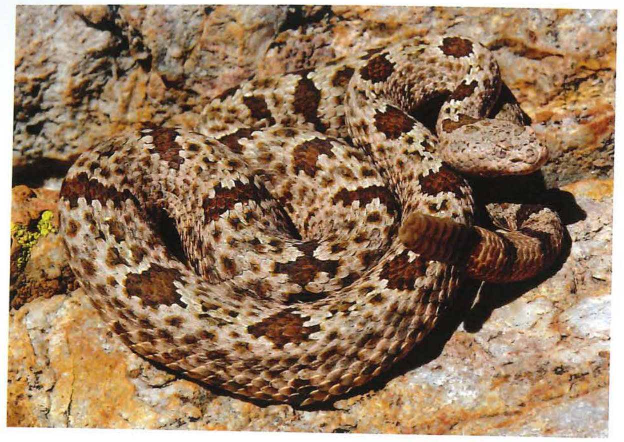

Figure 6. *Crotalus lepidus* (Rock Rattlesnake) from the Dragoon Mountains, Cochise Co. Photo by Kenny Sharrocks.

(usually 23) mid-body rows, and 14–20 (usually 17–18) rows near the tail (Ernst and Ernst 2012). *Crotalus l. klauberi* males have 152–172 ($\bar{x}$ = 162) ventrals and 20–29 ($\bar{x}$ = 25) subcaudals, whereas females have 155–170 ($\bar{x}$ = 161) ventrals and 16–24 ($\bar{x}$ = 20) subcaudals (Campbell and Lamar 2004). In a sample of *C. l. klauberi* from the Animas, Chiricahua, and Peloncillo mountains, one of us (ATH) found that males had 19–32 subcaudals ($\bar{x}$ = 23.8 ± 1.7, *n* = 136) and females 16–24 subcaudals ($\bar{x}$ = 18.8 ± 1.6, *n* = 94). There are 10–13 ($\bar{x}$ = 11.4) rattle fringe scales in *C. l. klauberi* (Campbell and Lamar 2004). The cloacal scute is undivided.

Similar Species. *Crotalus willardi* and *C. pricei* are also small, montane rattlesnakes that co-occur with *C. lepidus* in some habitats and could conceivably be confused with it. However, both are readily differentiated by color and pattern. *Crotalus willardi* has pale crossbars bordered by darker ground coloration on the dorsum that separate reddish-brown to tan or gray rectangular blotches, as opposed to the black bands found on *C. lepidus*. Furthermore, *C. willardi* has a pronounced, upturned canthal ridge (see Figs. 1 and 2 in the *C. willardi* account), as opposed to the more rounded snout of *C. lepidus*. Finally, *C. w. willardi* has vivid white and reddish facial markings idiosyncratic to the subspecies that distinguish it from all other rattlesnakes. In the Peloncillo Mountains, both *C. w. obscurus* and *C. l. klauberi* are gray overall and have little to no facial markings, but they can be distinguished based on overall pattern and the presence or absence of the canthal ridge. *Crotalus pricei* has distinctive paired dark spots running the length of its dorsum, rather than dark crossbands. *Crotalus molossus* and *Crotalus cerberus* both attain a much larger size and are readily distinguished by overall color and pattern differences. *Crotalus molossus* is green with overtones of gray, brown, or yellow and has dark, diamond-shaped blotches (sometimes approaching crossbands). It also has a distinctive black tail and a black snout. *Crotalus cerberus* has dark blotches or is nearly uniformly black as an adult. Juvenile *C. cerberus* can be grayish, but they have blotches as opposed to bands. Although *Lampropeltis alterna* (Gray-banded Kingsnake) is not found in AZ, Garstka (1982) proposed that the "alterna phase" of *L. alterna* is a Batesian mimic of *C. lepidus* where their ranges overlap.

■ **Distribution and Abundance.** In México, *Crotalus lepidus* occurs in the Sierra Madre Occidental and on the northern Mexican Plateau (Campbell and Lamar 2004). In the United States, *C. lepidus* occupies rocky hills and mountain ranges in southwestern and south-central TX, southern NM, and in the sky island mountain ranges of southeastern AZ. *Crotalus l. klauberi*, the only subspecies in our state, ranges from southeastern AZ, southwestern NM, and extreme west TX (Franklin Mountains) south through the Mexican states of Chihuahua, eastern Sonora, and Durango to Zacatecas, Aguascalientes, Jalisco, and Michoacán (Heimes 2016). *Crotalus l. lepidus* is found from extreme southeastern NM (Guadalupe Mountains) and southwestern TX south through the Mexican states of Coahuila and far eastern Chihuahua to southern Tamaulipas and northern San Luis Potosí. *Crotalus l. maculosus* is found in Durango and Nayarit, México. However, genetic studies suggest that the haplogroup associated with *C. l. klauberi* across most of its range terminates in northern Durango, México, and the haplogroup associated with *C. l. lepidus* occupies southern Durango and southern Sinaloa (Bryson *et al.* 2011b).

Crotalus l. klauberi is the only subspecies found in AZ (Map 8). Vouchers document it in the Canelo Hills as well as the Chiricahua, Dos Cabezas, Dragoon, Huachuca, Peloncillo, Santa Rita, and Whetstone mountains. A recent photographic voucher (ASU HP00074) documents *C. l. klauberi* in the Patagonia Mountains.

Rangewide, *C. lepidus* is vertically distributed from *ca.* 300 to 3,000 m ASL (Campbell and Lamar 2004). In AZ, it is found from 1,539 to 2,500 m ASL but is most common between 1,829 and 2,286 m ASL (Lowe *et al.* 1986). A recent voucher from the northern end of the Patagonia Mountains was found at 1,402 m ASL.

Questionable Localities. *Crotalus lepidus* occurs in most of the southeastern and southwestern groups of mountain ranges in the Madrean Archipelago (Bezy and Cole 2014). Although its absence from some western peripheral ranges (*e.g.*, Baboquivari and Pajarito mountains) is not particularly surprising, its absence from the Mule and Swisshelm mountains is biogeographically enigmatic. The Mule and Swisshelm mountains harbor typical habitat for the species, and both fall well within the species' overall distribution in AZ. Continuously occupied since its founding in 1880, the town of Bisbee sits at 1,688 m ASL in the Mule Mountains in the midst of what appears to be completely appropriate habitat for *C. lepidus*. Bisbee has been a hub of mining activity and tourism for well over a century and has been the Cochise Co. seat since 1929. Nevertheless, there are no vouchers or reliable sightings of *C. lepidus* in the Mule Mountains. Although there have been no systematic herpetological surveys of the Mule Mountains, it seems likely a report or specimen would have appeared in the last 140 years if the species was present. By contrast, although the Swisshelm Mountains also lack vouchers, they have seen far less human activity and, given their proximity to the Chiricahua Mountains, might hold an undocumented population. However, *C. lepidus* was not observed during 15 years of herpetological surveys (that included pitfall and funnel trapping) at the southern end of the Swisshelm Mountains on Leslie Canyon National Wildlife Refuge (W.R. Radke, pers. comm.). The Empire, Mustang, Pedregosa, and Perilla mountains of Cochise Co. might also harbor undocumented populations.

Figure 7. *Crotalus lepidus* (Rock Rattlesnake) from the Chiricahua Mountains, Cochise Co. Photo by Jim Rorabaugh.

Although this species does not appear to occupy any of the northern group of mountains in the Madrean Archipelago (Bezy and Cole 2014), there is an unvouchered sighting of *C. lepidus* in the Santa Teresa Mountains, Graham Co. in 2002 (S. Marlatt, pers. comm.). Unvouchered sightings of *C. lepidus* near Coalson Peak along the San Francisco River, Greenlee Co. (R. Phillips, pers. comm.) are plausible, given that vouchers have been collected in the San Francisco River watershed *ca.* 50 km to the east in NM (Degenhardt *et al.* 1996).

Status and Trends. Quantitative population estimates, population densities, and encounter rate data are lacking for this species. This is somewhat surprising, considering that five different field studies of *C. lepidus* have employed mark-recapture techniques (Beaupre 1995a; McCrystal *et al.* 1996; Prival 2008; Mata-Silva 2011), including studies conducted by ATH in the Animas, Chiricahua, and Peloncillo mountains. Johnson and Mills (1982) first summarized the status of *C. lepidus* in AZ and suggested that although

Figure 8. A neonatal *Crotalus lepidus* (Rock Rattlesnake) from the Santa Rita Mountains, Santa Cruz Co., with the typical yellow tail and button. Photo by Rye Jones.

some "populations are believed by Tucson area herpetologists, both professional and amateur, to have declined" (including Carr Canyon in the Huachuca Mountains and Madera Canyon in the Santa Rita Mountains), the species remains "fairly common over a substantial geographic area in its known and historic range in Arizona." Holm and Lowe (1995) reported collecting and killing of montane rattlesnakes in Scotia Canyon, Huachuca Mountains. Although there are over 40 known collecting sites in AZ (Johnson and Mills 1982), no extirpations have been reported. Whereas the viability of large populations does not appear to be at risk from collecting by hobbyists, small and isolated populations might be vulnerable to extirpation due to the ease with which *C. lepidus* is located and its life history traits.

Crotalus lepidus was commonly encountered during field studies in the Chiricahua (Prival 2008), Huachuca (McCrystal *et al.* 1996; Swann and Schwalbe 2002), and Whetstone (Turner *et al.* 1999, 2003) mountains in AZ, as well as in the Animas Mountains of NM (ATH, pers. obs.). Despite having received a fair amount of herpetological attention over the last century, including surveys for *C. lepidus* from 1991 to 1994 (McCrystal *et al.* 1996), *C. lepidus* was only recently documented in the Patagonia Mountains, suggesting that populations in this area are likely local or occur at very low densities. In the 1990s, one of us (ATH) conducted mark-recapture studies in the vicinity of Geronimo Trail in the Peloncillo Mountains and found that *C. lepidus* was not captured nearly as frequently there as in the adjacent Animas or Chiricahua mountains. In 2017, experienced field teams spent 829.5 person-hours (445.0 in August and 384.5 in late September and early October) searching for montane snakes in ideal habitat in Skeleton Canyon and its tributaries in the Peloncillo Mountains and found no *C. lepidus*, but did find 27 *C. molossus* and 1 *C. willardi* (Holycross and Christman 2018).

Anthropogenic disturbances to habitat include mining, grazing, road building, collecting, recreational development, and an altered role of fire in these ecosystems (Johnson and Mills 1982; Smith *et al.* 2001). Climate change could negatively affect populations by decreasing available habitat as the climate envelope on which *C. lepidus* relies shifts to higher elevations. The response of southwestern forests to climate change, especially with regard to alteration of the role of fire, is of particular concern (Dale *et al.* 2001; Smith *et al.* 2001; Williams *et al.* 2010; Falk 2013; Davis *et al.* 2015; Jones *et al.* 2016).

■ **Habitat.** Across its range, *C. lepidus* occupies plant communities ranging from peripheral Chihuahuan Desertscrub habitat (Axtell 1959) up into montane coniferous forests (Lowe *et al.* 1986), upper cloud forests (Armstrong and Murphy 1979), and Tropical Deciduous Forest (Ernst and Ernst 2012). In AZ, at the lower elevational range of *C. lepidus*, Semidesert or Plains grasslands meets Madrean Evergreen Oak Woodland (as in the Canelo Hills), and at the highest elevations, the habitat is Rocky Mountain Montane Forest (Lowe *et al.* 1986). However, in AZ the vast majority of *C. lepidus* are found in the Madrean Evergreen Woodland belt of our sky islands. Overstory plants include several species of trees, including Arizona white oak (*Quercus arizonica*), Arizona blue oak (*Q. oblongifolia*), Emory oak (*Q. emoryi*), gray oak (*Q. grisea*), silverleaf oak (*Q. hypoleucoides*), madrone (*Arbutus* sp.), alligator juniper (*Juniperus deppeana*), pinyon pine (*Pinus cembroides*), Chihuahua pine (*P. leiophylla*), and Apache pine (*P. engelmannii*). Riparian trees include Arizona sycamore (*Platanus wrightii*), Arizona walnut (*Juglans major*), box elder (*Acer negundo*), and velvet ash (*Fraxinus velutina*). Agave is often present in the understory, as are Wright's silktassel (*Garrya wrightii*) and manzanitas (*Arctostaphylos* spp.).

Rock Rattlesnakes are aptly named, as they are most often found among rock features in the communities they occupy. These include outcrops, rocky slopes, boulder piles, and rocky stream banks. Talus slopes often yield more captures than adjacent habitat, especially talus composed of baseball- to softball-sized rocks (Beaupre 1995a; McCrystal *et al.* 1996; Prival 2008). Talus slides offer both fine-scale thermoregulation within the vertical strata of the slide and opportunity to forage on a commonly consumed prey species, *Sceloporus jarrovii* (Yarrow's Spiny Lizard). *Crotalus lepidus* is less frequently encountered away from rocks but does occupy and travel through adjacent habitats, particularly during periods of high humidity, after rainfall, or when gestating. Occasionally, we have found *C. lepidus* in open, grassy habitats hundreds of meters from substantial rock features; in these rare instances, the snakes are often associated with rodent burrows or other cover.

Prival (2008) found that males and non-gravid females were more often found on north-, northwest-, and northeast-facing slopes, whereas gravid females were more abundant on south-, southwest-, and west-facing slopes. Gravid females were also found farther from trees, in areas with less cover above 2 m high, and in places with more grass cover than males and non-gravid females. Gravid females were found most often in open, sunny areas dominated by bunchgrasses and bare soil, and about a third of the time in talus. Males and non-gravid females were found in talus most often, followed by shady areas covered in leaf litter and dense shrubs. Prival (2008) suggested that sexual dichromatism in the population he studied is an adaptation for crypsis that corresponds to differences in habitat used by these demographic groups. Mata-Silva (2011) quantified macrohabitat and microhabitat use by eight radio-tagged *C. l. lepidus* in Chihuahuan Desertscrub habitats in west TX.

Figure 9. A putative natural hybrid between *Crotalus lepidus* (Rock Rattlesnake) and *Crotalus willardi* (Ridge-nosed Rattlesnake) from the Santa Rita Mountains, Santa Cruz Co. Photo by Brendan O'Connor.

■ **Diet and Foraging Biology.** Rangewide, *C. lepidus* has a varied diet, with some differences between subspecies and populations. This species is sometimes regarded as a lizard-eating specialist, but the presence of centipedes, mammals, and other prey in its diet suggests this is an oversimplification. Holycross *et al.* (2002a) described the diet of *C. l. klauberi* using samples collected from animals in the field, museum specimens, and published and unpublished reports. They identified 159 prey items of *C. l. klauberi* from the northern Sierra Madre Occidental and associated sky island mountain ranges in AZ, NM, Sonora, and Chihuahua. Diet consisted primarily of lizards (55%) and scolopendromorph centipedes (28%) but also included small mammals (14%), three birds (2%), and one snake (<1%). Approximately 92% of the lizards consumed were *Sceloporus*, and approximately 88% of these were identified as *S. jarrovii*. Lizard prey also included *Aspidoscelis* spp. (whiptails), *Sceloporus clarkii* (Clark's Spiny Lizard), *S. virgatus* (Striped Plateau Lizard), and *Urosaurus ornatus* (Ornate Tree Lizard). Proportions of major prey classes in the diet of this species were independent of mountain range, source of sample (stomach *vs.*

intestine/feces), sex, and age class. However, predator SVL differed significantly among prey classes. Snakes that ate birds had the longest mean SVL, followed sequentially by those that ate mammals, lizards, and centipedes. Mammals were not recorded in the diet of snakes <250 mm SVL. Centipedes were consumed later in the year than lizards, which may reflect prey activity patterns. Prey classes did not differ in elevation.

Although centipedes are prey for a number of snake species, including rattlesnakes (Holycross and Mackessy 2002; Holycross *et al.* 2002a,b), both the frequency with which large centipedes were consumed by *C. l. klauberi* and the relative size of predator and prey are surprising. For example, a 197 mm SVL *C. l. klauberi* (MVZ 229798) collected by H.W. Greene contained a 135 mm long centipede! Rattlesnakes may not always win this battle. One of us (ATH) examined a young *C. l. klauberi* (280 mm SVL; ASU 33115) found dead and slightly decayed on 1 July 1996 in the Animas Mountains. Two intact *Scolopendra* legs were found in its stomach, but no other remains were found in the gastrointestinal tract. In addition, several *Scolopendra* tarsi were removed from muscle tissue just inside a small epidermal rip on the snake's neck. In Sunnyside Canyon in the Huachuca Mountains, a juvenile *C. lepidus* was found writhing and plainly injured next to the freshly regurgitated remains of a centipede only slightly smaller than the snake; the next day, the snake was found dead a few inches from where it was first observed (S. Hale, pers. comm.). Centipedes are venomous, and the venom of *S. heros* (Giant Desert Centipede) is quite toxic to mammals, including humans, who sometimes have significant systemic reactions to envenomation (LLCJ, pers. obs.). The centipedes in Holycross *et al.* (2002a) were not identified beyond genus (*Scolopendra*), but were likely *S. heros*, *S. polymorpha* (Common Desert Centipede), or some of each.

Beaupre (1995a) studied the diet and natural history of two populations of *C. l. lepidus* from different elevations in Big Bend National Park, TX. Animals from the low-elevation site preyed on mammals more than reptiles, while the situation was reversed for the higher-elevation site. Lizards included *Aspidoscelis* spp., *Cophosaurus texanus* (Greater Earless Lizard), *Sceloporus merriami* (Canyon Lizard), and *U. ornatus*. Mammal prey included *Dipodomys* spp. (kangaroo rats), *Perognathus* spp. (pocket mice), *Peromyscus* spp. (deer mice), and *Sigmodon* spp. (cotton rats). Although most of these species occurred at both sites, there were differences in the structure of the community of available prey. One notable difference between the studies of Holycross *et al.* (2002a) and Beaupre (1995a) is the conspicuous lack of centipedes in the latter study. *Sceloporus torquatus* (Crevice Swift), *Phrynosoma orbiculare* (Mountain Horned Lizard), and *Lampropeltis greeri* (Greer's Kingsnake) are reported from *C. lepidus* collected in Aguascalientes, México; the authors provide a summary of records of snake consumption (Carbajal-Márquez *et al.* 2012).

Lazcano *et al.* (2004) reported five additional observations of predation on lizards (genera *Barisia*, *Plestiodon*, and *Sceloporus*) by *C. l. lepidus* and *C. morulus*. Bryson *et al.* (2002a) reported *Anolis nebulosus* (Clouded Anole), *S. jarrovii*, and an unidentified mammal in the diet of *C. l. maculosus*. Lizards (*Aspidoscelis*, *Phrynosoma*, and *Urosaurus* spp.), snakes (*Gyalopion canum*), and frogs (*Eleutherodactylus marnockii*, Cliff Chirping Frog) have been recorded as prey in Terrell Co., TX (Milstead *in* Werler and Dixon 2000).

Captives have consumed a variety of animals, including anurans (Falck 1940), crickets (McCrystal *et al.* 1996), lizards (*Sceloporus undulatus*, Eastern Fence Lizard, and *Anolis carolinensis*, Green Anole), laboratory mice (Kauffeld 1943a), and conspecifics (Williamson 1971; Harris and Simmons 1977). Mata-Silva *et al.* (2014) documented *C. l. lepidus* harvesting rainwater in the Chihuahuan Desert.

Crotalus lepidus is primarily an ambush predator. When ambush hunting for saxicolous lizards, *C. lepidus* is often found in a loose, S-shaped posture on the side of a rock, or in an open, vertical crack in a rock, with the head directed toward the lip of the rock (Beaupre 1995a; McCrystal *et al.* 1996; Holycross *et al.* 2002a). Juveniles have a vivid yellowish-orange tail that they use to lure lizard prey (Fig. 8; Kauffeld 1943b; Neill 1960; Starrett and Holycross 2002).

In laboratory experiments, Chiszar *et al.* (1986b) found that *C. l. klauberi* would strike and hold onto lizard prey until it was immobilized, whereas mammalian prey were bitten, released, and then tracked with the tongue and vomeronasal organ. This pattern is typical of pit vipers, since most mammals have greater ability to turn on their attacker with tooth and claw if retained in the mouth. In these experiments, *C. l. klauberi* was less effective than *C. v. viridis* (a species that relies more on rodent prey) in its ability to trail mammal prey.

■ **Predators and Parasites.** Predators of *C. lepidus* in nature are poorly documented. Klauber (1972) reported a collared lizard (*Crotaphytus* sp.) that grasped a *C. lepidus*. Ernst and Ernst (2012) provided a summary list of likely predators that included ophiophagous snakes, birds of prey, and carnivorous mammals. In a study of *Nasua narica* (White-nosed Coati) in the Chiricahua Mountains, several coati scats contained *C. lepidus* remains, and an adult female coati was observed biting and swallowing a *ca.* 30 cm long *C. lepidus*, starting from the head (J. Koprowski, pers. comm.). Four of 10 radio-tagged *C. l. lepidus* were killed by unknown predators on a reserve in Hudspeth Co., TX (Mata-Silva 2011).

Goldberg and Bursey (1999) found that 5% of the 55 *C. lepidus* they examined were infected with larval spiny-headed worms (phylum Acanthocephala). Goldberg *et al.* (2002a) reported the nematode *Abbreviata terrapenis*, normally a parasite of the lizard genera *Sceloporus* and *Aspidoscelis*, as an accidental parasite occasionally present in the stomach, intestine, and feces of *C. lepidus*. The nematode *Physocephalus sexalatus* was reported by McAllister *et al.* (2004). Rodriguez and Lazcano (1992) reported the snake mite *Ophionyssus natricis* from captive *C. lepidus*. Reddacliff *et al.* (1993) reported mortality in three captive *C. l. klauberi* from systemic yeast infections; two of the three snakes had concomitant bacterial infections. *Crotalus lepidus* has been known to die from an ophidian paramyxovirus-like infection in captivity (Jacobson *et al.* 1980). Hilman and Strandtmann (1960) examined a *C. lepidus* from west TX infected by the blood protozoan *Hepatozoon serpentium*.

■ **Behavior.** In the United States, *C. lepidus* is active from March into October (Beaupre 1995a; Degenhardt *et al.* 1996; Ernst and Ernst 2012), although in AZ, it is most readily observed during the monsoon (July to mid-September). From late May through June, *C. lepidus* is less frequently encountered aboveground during the day, and in our experience, many of the animals found during this period are basking, gravid females. November through February is spent hibernating in subterranean refugia, although we have observed snakes basking at the mouth of burrows or beside rock piles in winter. In spring and fall, when temperatures are relatively mild, *C. lepidus* is primarily diurnal. During the hotter summer months, we have found them throughout the day, but we find them most often during the morning. They have also been found on the surface at all hours of the night. In our experience, *C. lepidus* spends more time on the surface in the days following summer showers. It seems especially active on sunny mornings following nighttime rains (Armstrong and Murphy 1979; Lowe *et al.* 1986; Prival 2008). Not only do rains moderate the temperature, but they also appear to increase lizard surface activity. *Scolopendra* centipedes are also most active during the monsoon when humidity is high (Schmidt in Holycross *et al.* 2002a).

Capture data from studies conducted by ATH in the Chiricahua, Peloncillo, and Animas mountains shed some light on when snakes have been successfully found aboveground. Diel distribution of search effort varied seasonally in these studies, although almost all searching was conducted during daylight hours. Therefore, these data reflect both the distribution of search effort and the activity patterns of snakes. All 43 *C. lepidus* caught from May to mid-June were captured between 1000 and 1930 h, and captures were evenly distributed throughout this time frame.

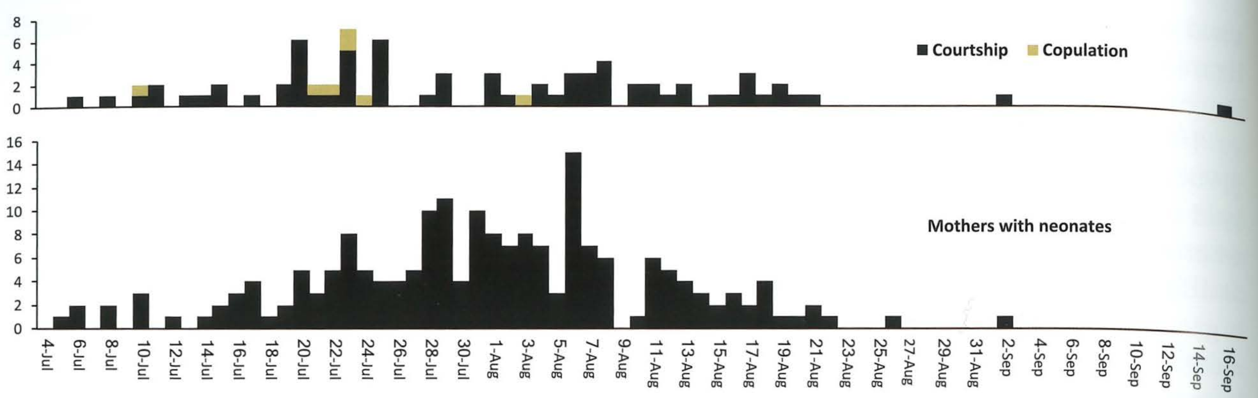

FIGURE 10. Distribution of observations of courtship ($n = 71$), copulation ($n = 7$), and mothers attending neonates ($n = 194$) by date in wild *Crotalus lepidus klauberi* (Banded Rock Rattlesnake) in the Huachuca Mountains, Cochise Co. All observations were made by John P. Porter from 1983 to 2018.

In July and August, 90 of 95 captures occurred between 0700 and 2000 h, although precisely 50% of these occurred between 0700 and 1100 h. Five individuals were found after nightfall in July and August. From September through the first week in October, 72 of 74 captures occurred between 0900 and 1700 h, while two occurred slightly after dark. On 18 November 1996, one of us (ATH) recorded a female *C. lepidus* basking at 1330 h.

Field body temperatures of *C. lepidus* are 21–38 °C when surface active, but their body temperatures are usually 25–30 °C (Klauber 1972; Beaupre 1995b). In AZ, McCrystal *et al.* (1996) calculated a mean body temperature of 25.2 °C and a mean surface temperature of 22.0 °C. These temperatures were not significantly different from those recorded for *C. willardi* at the same study site.

McCrystal *et al.* (1996) also recorded the position of *C. l. klauberi* when first encountered. The snakes were most often detected by their rattling and movement when fleeing the researchers (23%), rattling from under surface objects (20%), and crawling on the surface (14%). They were also discovered while basking (12%) and in a hunting position (11%). Other less frequent positions included flight without rattling, coiled, and elongate but immobile. Their primary line of defense seems to be crypsis, then flight, as they slip into cracks or the subterranean realm of talus cavities. They usually do this while rattling, which is how researchers often discover them. They typically descend into talus until they are just out of sight but continue deeper into the talus if pursued. *Crotalus lepidus* sometimes assumes a defensive coil and rattles without retreating but is more apt to flee than many larger rattlesnakes. Striking and biting appear to be defenses of last resort.

Studies of *C. lepidus* spatial activity using radio-telemetry have been conducted in the Peloncillo Mountains (AZ and NM; Smith *et al.* 2001) and in TX by Beaupre (1995a) and Mata Silva (2011). Smith *et al.* (2001) conducted a short-term prescribed fire monitoring study from 5 May to 31 July 1997 in the Peloncillo Mountains (AZ and NM). The five radio-tracked *C. l. klauberi* moved from 1.3 to 36 m/day, and total activity area ranged from 1.3 to 1,454 m^2. Smith *et al.* (2001) also included *C. molossus* and *C. willardi* in their study and found that as a group, these three species of rattlesnake moved less frequently and were in subterranean retreats (during the day) more often after the fire. However, spatial descriptors of activity did not significantly differ before *vs.* after the fire, suggesting that in recently burned landscapes, montane rattlesnakes might shift to nocturnal movement to avoid detection by predators and/or to avoid higher substrate temperatures.

In Big Bend National Park, 13 male *C. l. lepidus* were radio-tracked over a five-year period and moved an average of 20.4 ± 3.0 m/day ($n = 32$), and distance moved per day did not significantly differ among the summer months (Beaupre 1995a). In the Chihuahuan Desert (Hudspeth Co, TX), *C. l. lepidus* were radio-tracked from 2007 to 2010 (Mata-Silva 2011). Minimum convex polygon estimates of occupied home ranges for six males were 6.9–29.1 ha ($\bar{x} = 15.8$ ha) and for two females 6.4 and 8.2 ha. Core activity areas based on 50% kernels were estimated at 1.8–6.1 ha ($\bar{x} = 3.3$) for males and 1.4 ha and 1.6 ha for females. Average distance moved per day by each snake (calculated including days the snakes did not move) were 3.6–15.8 m and averaged 8.5 m over all eight snakes tracked. Although monthly movement rates did not statistically differ, snakes exhibited the "highest average movement rates in September, followed by June, July and August" (Mata-Silva 2011).

Arboreal behavior has occasionally been documented (Rossi and Feldner 1993; Swann and Bell 1999). Frey (1996) observed a *C. l. klauberi* submerged in 0.5 m of water in an ambush posture over a deeper part of a pool containing fish and suggested the snake was either thermoregulating (cooling off on a hot day) or foraging for fish in the creek. Fish are not known from the diet of *C. lepidus*.

FIGURE 11. An adult female and an adult male *Crotalus lepidus* (Rock Rattlesnake) found with four neonates on 10 August 2010, in the Canelo Hills, Santa Cruz Co. Photo by Kenny Sharrocks.

REPRODUCTION. In AZ populations of *C. l. klauberi*, courtship, copulation, and parturition all take place primarily during July and August and rarely into early September (Fig. 10). One of us (ATH) recorded courtship in *C. l. klauberi* on 27 July in the Peloncillo Mountains and found a pair together on 9 October in the Animas Mountains. Although Prival (2008) did not observe courtship or copulation during his study in the Chiricahua Mountains, he did find male and female snakes together on 25 July, 20 August, and 21 August. In the Huachuca Mountains, McCrystal *et al.* (1996) found males and females together on 11 March, 30 July, 14 September, and twice on 20 September. A male and female *C. l. klauberi* were also found together on 15 July in the Cookes Range, Luna Co., NM (Swinford 1990). Presumed mating associations in July and August have been reported for *C. l. lepidus* in Big Bend National Park (Beaupre in Goldberg 2000c), and six observations of *C. l. lepidus* "courtship and mating behavior" were made during August and September in Hudspeth Co., TX (Mata-Silva 2011). Captive *C. l. klauberi* from the Sierra del Nido, Chihuahua, México, were observed in courtship on three occasions between 14 and 28 September 1977 (Guese *in* Armstrong and Murphy 1979). Barker (*in* Armstrong and Murphy 1979) observed a pair of *C. l. klauberi* courting on 11 October 1977, although it is unclear whether the observation was of captive or wild animals.

Prival and Porter (2016) reported combat between males "during the mating season," but the number of observations and specific dates were not noted. In correspondence with us, John P. Porter reported having only observed combat once (on 24 July 2008), which is noteworthy given his three decades of field work and the number of other reproductive behaviors he has observed (Fig. 10). In captivity, males engage in combat characteristic of many male pit vipers (Carpenter et al. 1976).

Females are capable of storing sperm (Dancik *in* Schuett 1992) and may regularly do so over winter. Presumably, fertilization takes place upon ovulation in spring. Assuming ovulation and fertilization take place at or near spring emergence, gestation lasts 4–6 months until parturition. Eleven gravid females observed by Prival (2008) were found from 16 July to 16 August. In northern populations of *C. lepidus*, young are born during the monsoon season in July and August (Fig. 10; Werler 1951; Prival 2008), when neonatal lizards and increased surface activity by *Scolopendra* spp. provide an abundant food resource for these small, gape-limited predators (Holycross *et al.* 2002a). Neonates stay with the mother for "about 11–14 days" and do not disperse until shortly after their first ecdysis (Prival 2008).

Litter size varies from one (Harris and Simmons 1972) up to eight in *C. lepidus* but is typically about four (Armstrong and Murphy 1979; Ernst and Ernst 2003; Prival 2008). Mean litter size for a population in the Huachuca Mountains was 3.6 neonates (*n* = 151 litters), and over half (56%) of these litters consisted of three or four neonates (Prival and Porter 2016). In west TX, Beaupre (1995a) reported litter sizes of 2–5 ($\bar{x}$ = 3.6 ± 0.31, *n* = 10), and neonates appeared as early as 15 July. A postpartum female was found with four neonates on 16 August 2007 in the Huachuca Mountains (C. Cochran and B. Starrett, pers. comm.). An adult female and an adult male were found with four neonates on 10 August 2010 in the Canelo Hills (Fig. 11). Another postpartum female was found with four neonates on 12 July 2016 in the Sierra Azul, Riva Palacio, Chihuahua, México, at 2,288 m ASL (R. Solís, pers. comm.). A captive pair of *C. l. klauberi* from the Organ Mountains, NM, gave birth to four neonates on 8 June 1988, and another captive pair from the Robledo Mountains, NM, gave birth to two neonates on 24 June 1988 (Swinford 1989, 1990).

Fifty-five percent of 20 adult female *C. l. klauberi* captured by Prival (2008) were gravid, suggesting that in AZ populations, females probably do not reproduce annually. Prival and Porter (2016) reported that females in the Huachuca Mountains give birth every two to three years, citing John Porter's unpublished data. In two populations in Big Bend National Park, Beaupre (1995a) reported 27% (*n* = 18) and 29% (*n* = 17) of females were gravid. However, Beaupre (1995a) also reported annual reproduction by one wild female *C. l. lepidus* over three consecutive years.

Goldberg (2000c) provided data from histological examination of 18 males and 18 females sampled from throughout the distribution of *C. lepidus*. Males with regressed testes were observed in May, June, and October, and spermiogenesis was documented June–October, with a peak July–September. All 15 males examined May–October had enlarged sexual segment of the kidney with secretory granules present. The smallest male undergoing spermiogenesis measured 352 mm SVL. Females in early stages of secondary yolk deposition were observed in July, August, and October. Females evidencing advanced secondary yolk deposition (follicles >6 mm long) were observed in August and October. A female with six oviductal embryos was collected 19 April, and pregnant females were observed in May and July (Goldberg 2000c). The smallest reproductively active female measured by Goldberg (2000c) was 340 mm SVL, although Prival (2008) reported a 332 mm SVL (367 mm TL) gravid female.

■ **REMARKS.** The diploid karyotype has 36 chromosomes, with 16 macrochromosomes and 20 microchromosomes (Baker *et al.* 1972). A *C. l. klauberi* acquired by W.H. Woodin as an adult on 7 July 1952 died on 6 March 1986, living 33 y and 7 mo in captivity (Slavens and Slavens 1991). Prival and Porter (2016) reported a female *C. l. klauberi* in the Huachuca Mountains that was repeatedly observed over a period of 21 years and estimated to be 23 years old at the time she was last seen; this study used an encoded pattern recognition system and photography to identify individual snakes. Additional records for longevity in captivity and data on growth in captivity are summarized in Ernst and Ernst (2012). Although little is known of growth in the wild, mark-recapture data from the Peloncillo and Animas mountains (ATH) offer some insights (Fig. 12). A male captured 19 August 1995 and PIT-tagged as an adult (341 mm SVL) was recaptured on 10 October 1998 and again on 2 October 2005, 10 y and 1 mo after his first capture.

Across its range, *C. lepidus* varies considerably in venom composition (Minton 1977; Glenn and Straight 1982, 1987; Rael *et al.* 1992; Forstner *et al.* 1997; (Gandara, abstract *in* 2011 Biology of the Rattlesnake Symposium Proceedings); Borja *et al.* 2013; Martínez-Romero *et al.* 2013; Rivas-Mercado 2014; Saviola *et al.* 2017). Among venomous snakes, inter- and intraspecific variation in venom composition sometimes relates to diet, and might track ontogenetic shifts in diet (Mackessy 1988; Barlow *et al.* 2009; Martinez-Romero *et al.* 2013). *Crotalus lepidus* venom (depending on location) includes Type I and/or Type II fractions, which may variously target invertebrates *vs.* vertebrates, and among vertebrates, reptiles *vs.* mammals. Northern subspecies (*C. l. lepidus* and *C. l. klauberi*) lacked metalloproteinases and were more toxic to lizards, while *C. l. maculosus* and *C. morulus* had metalloproteinases and were more toxic to mammals (Gandara 2011, *op. cit.*). All subspecies are cytotoxic. Ernst and Ernst (2012) summarized several studies on venom yield. *Crotalus l. klauberi* venom yield has been reported to be as high as 129 mg dry weight (Glenn and Straight 1982). However, other studies suggest 10–34 mg dry weight is more typical for adults (Klauber 1972; Minton 1977).

Bites to humans are infrequently documented, and in most cases were associated with intentional handling. Burch *et al.* (1988) and Hardy (1992) briefly mentioned envenomation by *C. lepidus*, although the latter case did not involve intentional handling. Wright and Wright (1957) and Klauber (1972) also described human envenomation. Norris (2005) reported a bite by *C. l. lepidus* from a captive specimen. One interesting case involved a professional herpetologist who was surveying for reptiles and amphibians when he was bitten by a *C. l. klauberi* that was unseen in a tree cavity as he passed by; he never touched the tree, but apparently passed close enough for the snake to feel threatened and strike (Swann and Bell 1999).

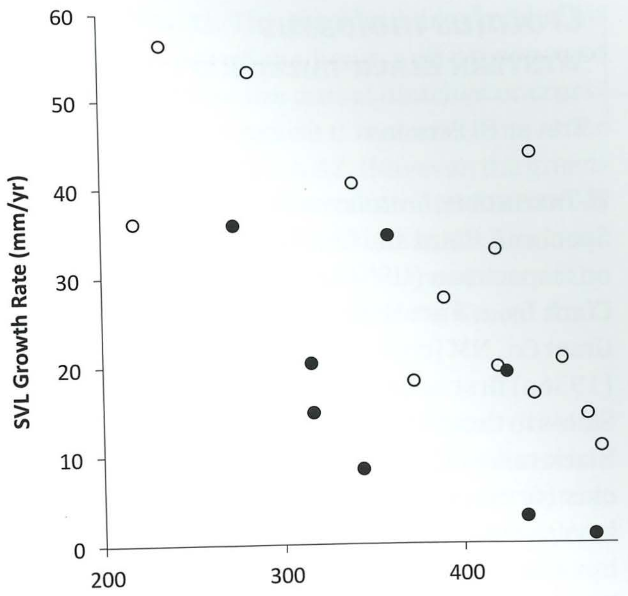

FIGURE 12. Growth rate in SVL (mm/year) as a function of initial SVL (mm) for 9 male (○) and 7 female (●) individual *Crotalus lepidus klauberi* (Banded Rock Rattlesnake) marked and recaptured in the Animas (Hidalgo Co., NM) and Peloncillo (Cochise Co., AZ and Hidalgo Co., NM) mountains. One female and two males were recaptured twice, and another male was recaptured 3 times. Only recaptures spanning at least one overwintering period and >300 days apart are included. Time between captures was 321–2,628 days or 0.9–7.2 years ($\bar{x}$ = 998 days or 2.7 years). Data collected by ATH and colleagues from 1994 to 2004.

Early to Middle Pleistocene fossil *C. lepidus* have been identified from Curtis Ranch Fauna in Cochise Co. (Brattstrom 1955a). Differences in physiological ecology, body size, oxygen consumption, metabolic rate, energy budgets, and water flux between two populations of *C. l. lepidus* occupying different ecological environments were studied in Big Bend National Park (Beaupre 1993a,b, 1996).

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