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Natural History of the Twin-spotted Rattlesnake (*Crotalus pricei*) in the Southernmost Range of its Distribution

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***Abstract*.—The Twin-Spotted Rattlesnake (*Crotalus pricei*) is a small-bodied rattlesnake that inhabits mountain systems from the southwestern tip of the USA to central México. Despite its wide distributional range, there is scarce information about its natural history in many localities where it is found, including the population occurring in Aguascalientes, México, where fewer than 10 individuals have been reported since 1953. The goal of this study was to describe ecological and morphological aspects of *C. pricei* in the southernmost portion of its distributional range and compare them with what we currently know for this species. We conducted field surveys in 2019 and 2020 searching for individuals of *C. pricei* and we found 19 individuals. General characteristics of this population did not vary from what we know for *C. pricei*, although we found some morphological differences at the subspecies level. *Crotalus pricei* was more easily found in July, August, and September, and it was commonly associated with Pine and Oak Forest leaf litter. Its main activity periods during the day were from 1100 to 1600. Two females gave birth while they were held captive; one gave birth to four neonates, and the other just six unfertilized ova. The information presented here increases the ecological knowledge of the population of this species occurring in Aguascalientes, México.**

Key Words.—Aguascalientes; detection rate; ecology; México; morphology; reproduction; sexual dimorphism; Viperidae

Introduction

Despite México being the center of rattlesnake diversity (*Crotalus* and *Sistrurus*), there is a lack of biological information about many species, particularly those whose populations have been elusive (Armstrong and Murphy 1979; Campbell and Lamar 2004; Meik et al. 2007). Such is the case of the Twin-spotted Rattlesnake (*Crotalus pricei*); the species was described more than a century ago (Van Denburgh 1895; McCranie 1980), but there is almost no information for several populations in México, mostly because of habitat inaccessibility (Armstrong and Murphy 1979). *Crotalus pricei* is a small-bodied rattlesnake with sizes ranging from 130 to 650 mm in total length; the dorsal pattern is comprised of two rows of dark spots (sometimes fused), and the background varies from blue-gray to gray or pale brown (McCranie 1980). It inhabits places covered predominantly by Pine-oak Woodlands usually associated with rocky ridges and occasionally canyon bottoms, but it can also be found in grassy mountain valleys, basking in the open, moving across rocks, or coiled under rocks or vegetation (Armstrong and Murphy 1979; Prival et al. 2002; Bryson et al. 2011b; Grabowsky and Mackessy 2019). It can be found at elevations between 1860–3350 m and maximum population densities have been recorded at the higher elevations (Contreras-Lozano et al. 2012; Prival and Schroff 2012).

Crotalus pricei is protected by Mexican law in the Official Mexican Norm NOM-059-Semarnat-2010, under the category of Special Protection (Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT] 2010). The International Union for the Conservation of Nature (IUCN) has the species in the Least Concern category (Hammerson et al. 2007), and its estimated Environmental Vulnerability Score (EVS) is 14, placing it on the highest level of risk given by this scoring system (Wilson et al. 2013). Studies of *C. pricei* have dealt with its ecology (Prival et al. 2002; Prival and Schroff 2012), reproduction (Goldberg 2000), venom composition and effects (Minton and Weinstein 1984; Cruz et al. 1987; Grabowsky and Mackessy 2019), general biology (Axtell and Sabath 1963), and evolution (Bryson et al. 2011b), focused mostly on northern populations. Females reach sexual maturity at 330 mm snout-vent length (SVL) and males at 322 mm SVL (Goldberg 2000; Prival et al. 2002), although Klauber (1972) reported a gravid female measuring 301 mm total length. The species exhibits a biennial reproductive cycle with litter sizes ranging from three to nine individuals born between July and August (Armstrong and Murphy 1979; Goldberg 2000). The diet of *C. pricei* is comprised mainly of lizards of the genus *Sceloporus* (usually Yarrow's Spiny Lizard, *S. jarrovii*), but there are reports of mammalian and bird prey items and one case of cannibalism (Cruz et al. 1987; Prival et al. 2002; Prival and Schroff 2012; Grabowsky and Mackessy 2019).

The Mexican highlands are known for being one of the biodiversity hotspots of Earth and are recognized for their rattlesnake species richness, and they also are hypothesized as the center of origin for this group of snakes (Alvarado-Díaz and Campbell 2004; Place and Abramson 2004; Bryson et al. 2011a). This region is home to a large number of small-bodied montane rattlesnake species, including the *C. intermedius* group containing *C. pricei* (Armstrong and Murphy 1979; Alvarado-Díaz and Campbell 2004). There are two recognized subspecies of *C. pricei*: *C. p. miquihuanus*, which occurs in the Sierra Madre Oriental (SMOr; Fig. 1) in the confluence of the Mexican states of Coahuila, Nuevo León, Tamaulipas, and San Luis Potosí (Armstrong and Murphy 1979; Contreras-Lozano et al. 2012), and *C. p. pricei*, which inhabits the Sierra Madre Occidental (SMOc; Fig. 1) and adjacent sky islands in southeastern Arizona (USA) and the Mexican states of Sonora, Chihuahua, Durango, Zacatecas, Jalisco, and Aguascalientes (McCranie 1980; Bryson et al. 2011b; Prival and Schroff 2012). In México, *C. pricei* is probably the most common rattlesnake at higher elevations within its range, where it is sympatric with Ridge-Nosed Rattlesnakes (*C. willardi*), Rock Rattlesnakes (*C. lepidus*), and Black Tailed Rattlesnakes (*C. molossus*; Armstrong and Murphy 1979). Nonetheless, little is known about the conservation status, habitat use, behavior, ecology, natural history, and range limits of the subspecies of *C. pricei* in México (Prival and Schroff 2012; Grabowsky and Mackessy 2019).

The status of *C. pricei* in the Mexican state of Aguascalientes is especially uncertain, as it represents the southernmost population in the range of this species (Reyes-Velasco et al. 2012), inhabiting only the highest elevations in the Sierra Fría (a southern outlier of the SMOc) in the northwestern corner of the state (McCranie 1980; Carbajal-Márquez and Quintero-Díaz 2016). Despite intensive, long-term efforts to locate specimens of this species in Aguascalientes, few occurrences have been reported, it is considered a rare species in the state, and, as a consequence, there is little information about this population (Sigala-Rodríguez 2008; Carbajal-Márquez and Quintero-Díaz 2016). The first specimen of *C. pricei* for Aguascalientes was reported in 1953 and it was identified as *C. p. miquihuanus* (Klauber 1972). Some years later, Wilson and McCranie (1979) reported an additional specimen from Aguascalientes with characteristics of Mexican Smallhead Rattlesnake (*C. intermedius*) and proposed that it was an undescribed species of *Crotalus*. Based on data from this specimen and another subsequently collected in 1989, Campbell and Lamar (2004) determined that the population

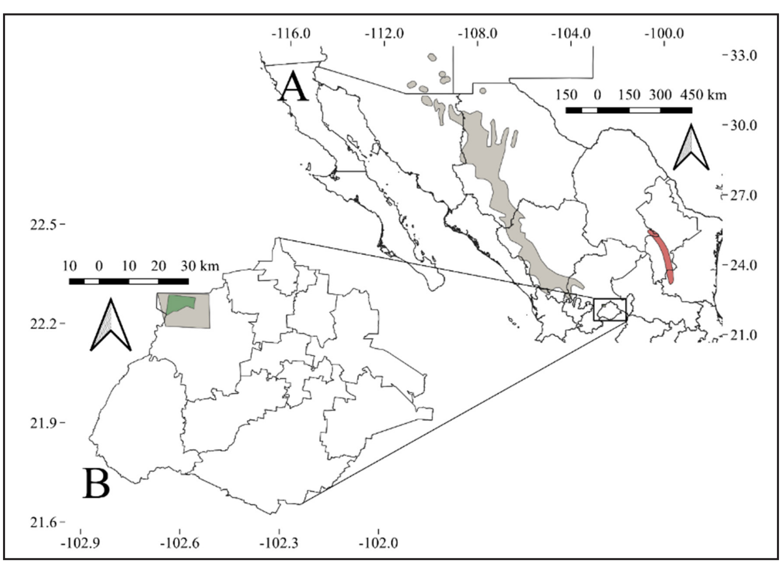

Figure 1. Distribution of the Twin-spotted Rattlesnake (*Crotalus pricei*) in southern USA and northern Mexico. (A) Map showing the distribution of the two recognized *Crotalus pricei* subspecies: *C. p. pricei* (gray), *C. p. miquihuanus* (red; modified from Campbell and Lamar 2004). (B) Localization of the study site (green) in the northwestern corner of Aguascalientes, México.

present in Aguascalientes represented *C. pricei*, but they could not determine whether it was *C. p. pricei* or *C. p. miquihuanus* because the characteristics of the few available specimens were a mix of both subspecies. Since then, data have been collected on several individuals (from this study and opportunistic encounters), and two vouchered specimens have been deposited in the Zoological Collection of the Universidad Autónoma de Aguascalientes (CZUAA).

Historically, much has been learned about rattlesnake biology through basic studies focused on questions related to natural history, diet, population size, ecology, or new records of rare species (Alvarado-Díaz and Campbell 2004; Lillywhite 2010; Mata-Silva et al. 2018). The aim of this study was to provide new information about the natural history of the population of *C. pricei* in Aguascalientes from recent field surveys. This information may serve as baseline for future research and may help to evaluate its local conservation status.

Materials and Methods

Study site.—Our survey area was inside Comunidad Indígena Monte Grande (Fig. 1), with about 3,600 ha in Sierra Fría (the southern extreme of the SMOc) in the municipality of San José de Gracia, Aguascalientes, México (22.26092°N, 102.6016°W; WGS84; 2,200–3,050 m elevation). Mean annual rainfall oscillates between 200–1,800 mm and mean temperature between 12°–18° C (Arriaga et al. 2000). The vegetation types present in Monte Grande are Oak Forest, Pine-oak Forest, Oak-juniper Forest, and Template Scrub, and the most common tree species in the area are Santa Rosa Oak (*Quercus sideroxyla*), Netleaf Oak (*Q. rugosa*), Potosi Oak (*Q. potosina*), Durango Pine (*Pinus duranguensis*), Chihuahuan Pine (*P. leiophylla*), Drooping Juniper (*Juniperus martinezii*), Alligator Juniper (*J. deppeana*), and Pointleaf Manzanita (*Arctostaphylos pungens*; Siqueiros-Delgado et al. 2016, 2017).

Survey design and data collection.—We focused our surveys in Pine-oak Forests, following previous studies on the ecology and distribution of the species (Prival et al. 2002; Bryson et al. 2011b), and used two decades of survey information and aerial photographs to identify potential sites to survey. Specifically, we sought out elevated areas (> 2,700 m elevation) with presence of Pine-oak Forest and rocky slopes. Once a potentially viable site was located, we conducted direct searches for rattlesnakes, trying to cover as much area as we could during the periods of time set each day depending on weather conditions. The searches took place weekly from June 2019 to December 2020 during 2–4 d per week, usually with a team of three people each week. Most of the searches were carried out during the mornings and evenings (0700–1900). The surveys included looking for snakes beneath trees and rocks, between the shrubs and bunchgrasses, among the leaf litter, and opportunistic sightings along transects. Night surveys also took place (2000–2300), but these where less frequent, and the time intervals varied each day depending on the weather conditions. With this information, we calculated survey effort, accounting for the total of search hours per person. To determine relative abundance, we divided the number of individuals encountered by the total of search hours to obtain the number of hours required to find one individual of *C. pricei* in the study site. We also recorded other rattlesnake species encountered.

When a rattlesnake was encountered, we captured and placed it in a herpetological bag. Later in the laboratory, we contained the snake using acrylic tubes to collect the following data: mass (M; in g), snout-vent length (SVL; ± 1 mm), tail length (TL; ± 1 mm), total length (T; ± 1 mm), head width (HW; ± 1 mm), head length (HL; ± 1 mm), number of dorsal spots (DS), and squamation, consisting of counting ventral scales (VE), subcaudal scales (SU), and intercanthal scales (ICS). We determined sex by cloacal probing or by everting hemipenes. We collected venom, fecal samples, and biological samples (blood and scale clips) for future studies. For measurements < 50 mm, we used a vernier caliper.

We used diagnostic characters described in the literature (Axtell and Sabath 1963; McCranie 1980; Campbell and Lamar 2004; Prival and Schroff 2012) such as number of VE, number of ICS, tail length-total length ratio (TL:T), and arrangement of dorsal spots to compare our individuals with geographic groups of *C. pricei.* For this, we divided *C. pricei* in four groups: our individuals, *C. p. pricei* SMOc North (approximate distribution), *C. p. pricei* SMOc South (approximate distribution), and *C. p. miquihuanus*, following the delineation presented in Bryson et al. (2011b). For the *C. p. pricei* SMOc South data, we used data in unpublished personal notes from L.M. Klauber from 1935 to 1954 provided by Harry W. Greene. For *C. p. pricei* SMOc North and *C. p. miquihuanus*, we used previously published information (Axtell and Sabath 1963; McCranie 1980; Campbell and Lamar 2004; Prival and Schroff 2012). For our data, besides the individuals we found in the field, we measured two individuals deposited in the Colección Zoológica de la Universidad Autónoma de Aguascalientes (UAAREP-290, UAAREP-377), one from the Universidad Autónoma de Nuevo León herpetological collection (UANL-4277), one from the University of Michigan Museum of Zoology (UMMZ-110878), and one measured in the field by us in 2009, for a total of 24 records. To determine activity patterns and habitat use, we recorded environmental data such as plant species, GPS coordinates, elevation, date, time, temperature, and humidity (approximately 1 m above ground level), canopy cover (using the cellphone application Canopeo from the Oklahoma State University), and behavior for every encounter. We marked all the snakes by painting the basal segment of the rattle with a unique combination of two colors. We kept the snakes for several days to allow them to defecate and for data acquisition, and subsequently released them in the same place where we found them.

Statistical analyses.—To determine if there is sexual dimorphism in *C. pricei*, we compared M, HW, HL, DS, SVL, TL, T, VE and SU between males and females. We also calculated the degree of sexual size dimorphism (SSD) in SVL following Gibbons and Lovich (1990) and Shine (1994). First, we used the Shapiro-Wilk test to evaluate if our data was normally distributed. For normally distributed data, we compared the characters using a Student *t*-test. For non-normal data, we used a Mann-Whitney U-test. For the statistical analyses, we only used adult individuals; males were considered adults at SVL ≥ 322 mm and females at SVL ≥ 330 mm (see Goldberg 2000; Prival et al. 2002). We conducted all statistical analyses using R version 3.6.3 (R Core Team 2020) with an alpha level of 0.05.

Results

Survey effort and detection rate.—From June 2019 to December 2020, we accumulated 1,111.5 search-hours, during which we were able to locate 19 *C. pricei* (Fig. 2), resulting in a detection rate of 0.017 snakes per search-hour, or one individual per 58.8 search-hours. If we consider only the months in which we found the species, effort decreases only slightly to 0.018 snakes per search-hour or 55.5 search-hours to find a snake. We also did this for every month (Table 1), revealing that the month with the highest detection rate was August, where 38.8 search-hours were required to find a snake. July, September, and November also had higher values than the overall detection rate (Table 1).

We found 45 rattlesnakes across all species during the survey period, with *C. pricei* representing 42.2% (19 records) of the total as the second most detected rattlesnake species in the area. *Crotalus lepidus* represented 53.3% (24 records) of the total, making it the most frequently detected species in the area. We only found two specimens of *C. molossus,* representing 4.5% of the total of records.

Figure 2. One of the 19 individuals of the Twin-spotted Rattlesnake (*Crotalus pricei*) that we found at the study site in Aguascalientes, México, 2020. (Photographed by Juan José Ayala Rodríguez).

Morphology and population structure.—From the 19 specimens assessed, 12 were adults (six males and six females) and seven were juveniles (two males and five females). Of the five individuals previously collected, four were adults (one male, three females) and one was a juvenile male. Morphological comparisons revealed two characters as sexually dimorphic (Table 2). We found significant difference in TL (t = -2.65, df = 11.224 P = 0.022), with males having longer tails, with measurements ranging between 44.14 ± 5.81 (standard deviation) mm for males and 36.56 ± 3.68 for females. We also found a significant difference in SU (t = -4.52, df = 10.839, P = 0.001) with males having more subcaudal scales (29.71 ± 2.98) than females (24.78 ± 1.64). The SSD index of -0.005 indicated that males were slightly larger than females.

As previously mentioned, there has been uncertainty in the assignment of individuals of *C. pricei* from Aguascalientes to one of the two recognized subspecies (*C. p. pricei* and *C. p. miquihuanus*) using morphological characters. There were not remarkable differences between the characteristics of *C. p. pricei* SMOc North (n = 304) and *C. p. pricei* SMOc South (n = 16; Table 3). The number of VE of female individuals from Aguascalientes (n = 24) overlapped with the known data for *C. p. miquihuanus* (n = 3), and the number of VE

Table 1. Search effort, detection rate, and the required search-hours to find a Twin-spotted Rattlesnake (*Crotalus pricei*) by month in Aguascalientes, México, 2019–2020. Only the months when snakes were detected are included.

Month	Search-hours	Snakes found	Detection rate (snakes/search-hour)	Search-hours per snake
June	150	1	0.007	150
July	240.5	5	0.021	48.1
August	194	5	0.026	38.8
September	207	5	0.024	41.4
October	129	1	0.008	129
November	109	2	0.018	54.5

Table 2. Morphological differences between adult females (n = 9) and adult males (n = 7) of the Twin-spotted Rattlesnake (*Crotalus pricei*) from Aguascalientes, México. Abbreviations are M = mass (g), HW = head width (mm), HL = head length (mm), SVL = snout-vent length (mm), TL = tail length (mm), T = total length (mm), DS = dorsal spots, VE = number of ventral scales, SU = number of subcaudal scales, and SD = standard deviation. Significant differences ($P < 0.05$) designated by an asterisk (*).

Character	Sex	Mean ± SD	Range	test	*P*-value
M	Male	37.6 ± 18.97	19–73	$U = 18$	1.00
	Female	34.3 ± 9.42	26–48		
HW	Male	12.1 ± 1.54	10.0–13.6	$t = -0.539$	0.600
	Female	11.5 ± 0.92	10.6–13.5		
HL	Male	19.8 ± 3.61	16.4–27.2	$t = -0.189$	0.855
	Female	19.2 ± 1.01	17.8–20.6		
SVL	Male	368.4 ± 37.03	336–446	$U = 42$	0.596
	Female	366.3 ± 24.92	335–400		
TL	Male	44.1 ± 5.81	2–34	$t = -2.65$	0.022*
	Female	36.6 ± 3.68	3–31		
T	Male	412.6 ± 40.73	382–498	$U = 37.5$	0.923
	Female	402.9 ± 27.48	366–439		
DS	Male	49.3 ± 5.22	41–56	$t = 1.86$	0.084
	Female	54.6 ± 6.09	47–67		
VE	Male	149.1 ± 4.78	140–154	$U = 45$	0.409
	Female	152.0 ± 3.74	143–157		
SU	Male	29.7 ± 2.98	24–33	$t = -4.52$	0.001*
	Female	24.8 ± 1.64	22–27		

in male individuals overlapped with the known data for *C. p. pricei* (Table 3). The number of ICS overlapped with the two subspecies and the DS arrangement is more similar to *C. p. miquihuanus*. Finally, the TL:T ratio resulted in differences among four groups, with *C. p. pricei* SMOc North having the smallest ratio (0.08) and *C. p. miquihuanus* with the largest (0.114); *C. p. pricei* SMOc South and *C. pricei* from Aguascalientes had intermediate values (0.084 and 0.098, respectively).

Activity patterns and habitat use.—We encountered *C. pricei* from June to November (Fig. 3) and the months with the most records were July, August, and September, when we found five snakes in each month. We found individuals of *C. pricei* from 1000–1800 with two activity peaks between 1201–1600 (Fig. 4), where we were able to locate 16 of the 19 snakes. The average air temperature at which we found snakes was 23.02° ± 4.16° C (range, 17°–30.1° C), the mean relative humidity was 48.1% ± 17.64 (range, 19–68%), and the canopy cover was 5.54% ± 3.81 (range, 0.03%–11.8%). All individuals were located no farther than 10 m from temporary streams: five of them were actively moving on leaf litter; 12 were coiled among leaf litter (pine and oak) or bunchgrass; and

Table 3. Comparison of morphological characters among Twin-spotted Rattlesnake (*Crotalus pricei*) populations across its range: SMOc North = *C. p. pricei* from the northern end of the Sierra Madre Occidental, Mexico; SMOc South = *C. p. pricei* from the central and southern end of the Sierra Madre Occidental, Mexico; this study = *C. pricei* from the southern end of the Sierra Madre Occidental in Comunidad Indigena Monte Grande, Aguascalientes, Mexico; *C. p. miquihuanus* in the Sierra Madre Oriental (SMOr). Data for SMOc North from McCranie (1980), Campbell and Lamar (2004), and Prival and Schroff (2012), for SMOc South from unpublished personal notes from L.M. Klauber (1935–1954), and for *C. p. miquihuanus* from Axtell and Sabath (1963), McCranie (1980), and Campbell and Lamar (2004). Abbreviations are VE = number of ventral scales, ICS = intercanthal scales, TL:T = tail length:total length ratio, DS = dorsal spots, and NA = information not available.

Character	SMOc North n = 304	SMOc South n = 16	this study n = 24	*C. p. miquihuanus* n = 3
VE (females)	157–171	157–163	143–153	143–145
VE (males)	149–162	153–163	148–156	135–141
ICS	0–9 (usually 4–6)	4	2–4	0–3
TL:T	0.08	0.084	0.098	0.114
DS	Generally separated	NA	Generally fused	Generally fused

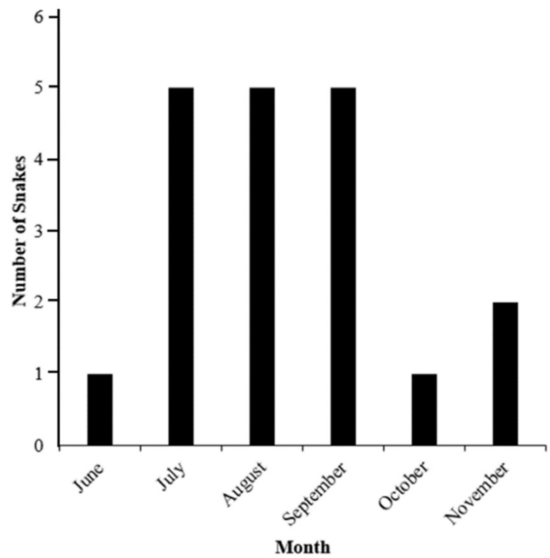

Figure 3. Number of Twin-spotted Rattlesnakes (*Crotalus pricei*) found per month at Aguascalientes, México, 2019–2020.

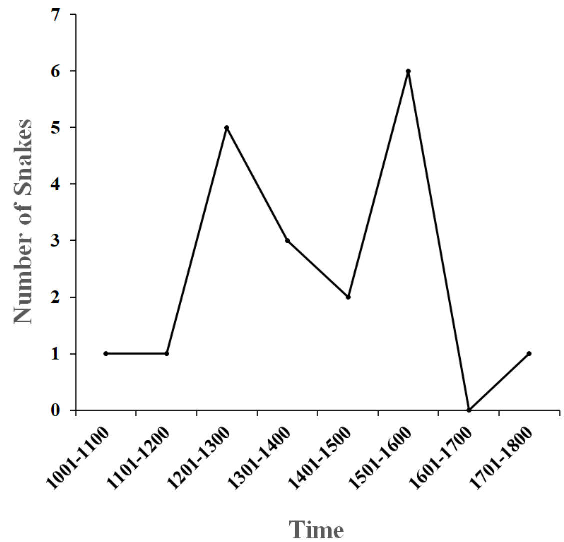

Figure 4. Number of the Twin-spotted Rattlesnake (*Crotalus pricei*) found per hour interval in Aguascalientes, Mexico, 2019–2020.

two of them were basking in open rocky areas. There were 11 plant species associated with the specimens of *C. pricei* (Fig. 5): Red Oak (*Quercus jonessi*), *Pinus duranguensis*, and muhly grass (*Muhlenbergia* sp.) were the most common species.

Notes on reproduction and behavior.—One female encountered during the surveys gave birth in the lab to four neonates 12 August 2020 during the time we held it to obtain measurements and biological samples. Another female deposited six unfertilized ova 28 August 2020. Most of the individuals of *C. pricei* that we found behaved quite peacefully in comparison with the snakes of other species present in the area (*C. lepidus* and *C. molossus*). Only two individuals of *C. pricei* struck the herpetological hook while being manipulated. When first encountered, the individuals of *C. pricei* would stay coiled in the substrate and some of them would try to escape among the leaf litter or shrubs, sometimes rattling for a few seconds. The same behavior was observed upon release of the individuals.

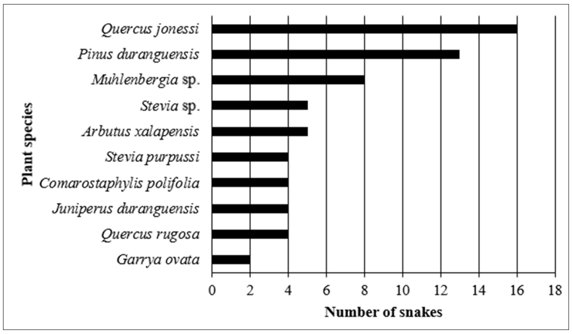

Figure 5. The number of Twin-spotted Rattlesnake (*Crotalus pricei*) found associated with different plant species in Aguascalientes, México, 2019–2020. Plant species are Red Oak (*Quercus jonessi*), Durango Pine (*Pinus durangensis*), muhly grass (*Muhlenbergia* sp.), stevia (*Stevia* sp.), Texas Madrone (*Arbutus xalapensis*), Hierba Dulce (*Stevia purpussi*), Madrone (*Comarostaphylis polifolia*), Durango Juniper (*Juniperus duranguensis*), Netleaf Oak (*Quercus rugosa*), and Eggleaf Silktassel (*Garrya ovata*).

Discussion

Survey effort and detection rate.—Our study represents the first data systematically gathered for *C. pricei* in Aguascalientes. The first specimen in Aguascalientes was collected in 1953 by E.T. Hooper (UMMZ–110878). The second was collected by I.E. Pinedo-Rodríguez in 1983 (UANL–4277) and Campbell and Lamar (1989) commented on the identity of the individuals from 1953 and 1983. The third recorded specimen was collected by V. Villalobos-Sánchez in 1998 (UAA–REP–290), while two more individuals were found but not collected in 2004 by H. Bárcenas and 2009 by R. Valencia-Villegas. The last recorded specimen before this study was found by R. Reyes-Ardit in 2011 (UAA–REP–377), all this despite intensive efforts made to find more individuals (Sigala-Rodríguez 2008).

Considering the scarcity of previous records, it was surprising that 19 individuals were encountered, given that the species is considered one of the rarest rattlesnakes in Aguascalientes (Vázquez-Díaz and Quintero-Díaz 2005; Sigala-Rodríguez 2008; Carbajal-Márquez and Quintero-Díaz 2016). In contrast, Armstrong and Murphy (1979) stated that *C. pricei* is probably the most common rattlesnake at higher elevations within its range, which is consistent with our sampling effort being concentrated in Pine-oak Forest, which are usually the locations with highest elevation in the study area. Another idea worth considering is that climate change and human perturbation might be restricting *C. pricei* to these few areas with the highest elevation within the limits of its distribution, as has been the case for other similar species (Davis et al. 2015); hence, the reason why other species of rattlesnakes (probably more tolerant of these changes) appear to be more common in lower elevations and *C. pricei* is only found at high elevations. During our study period, we found almost the same number of individuals of *C. lepidus* (24) as *C. pricei*, but just two *C. molossus* specimens. We expected to find more rattlesnakes of those species and just a few of *C. pricei* because the former two tend to be more common at lower elevations in the study area (Vázquez-Díaz and Quintero-Díaz 2005). We assume that the low numbers of individuals of *C. pricei* is because we were at the limits of its southern distributional range, so we did not expect it to be as frequent as in other areas where it occurs (Gaston 2000). Additionally, the population is numerically small, occupies a restricted area in Aguascalientes, and with limited prior information on its natural history in this Mexican State, in stark contrast with the populations that occur in the northern limits of its distribution, where the species is more abundant and occurs in four mountain systems (Prival and Schroff 2012).

Although we surveyed eight places in Monte Grande and found at least one *C. lepidus* in six of them, we located all *C. pricei* individuals in but one of the eight sites within an area of 10 ha. Therefore, it is difficult to estimate the population size of *C. pricei* in the study area, as they tend to concentrate into semi-discrete populations instead of being uniformly distributed throughout the landscape (Prival and Schroff 2012). This is also consistent with the small home range reported for this species: 0.16 ha for females and 2.29 ha for males (Prival et al. 2002). The effort needed to find *C. pricei* in Monte Grande (55.5 search-hours per snake) is further evidence of the low abundance of the species in the study area, particularly if compared with the study of Prival and Schroff (2012) in the Chiricahua Mountains in Arizona, USA, where they reported an encounter rate of one *C. pricei* every eight search-hours in one of their sites and 4.7 search-hours per snake in the other. This information is important for species with low capture rates, as it can help differentiate between true rarity and inadequate sampling (Shelton et al. 2017) and stresses the importance of local studies instead of just generalizing and extrapolating from studies in other areas. In the case of *C. pricei* from Aguascalientes, we can confirm that it is indeed a rare species, given the difference in the encounter rate between our results and the ones presented by Prival and Schroff (2012); however, more monitoring of this population would confirm increases or decreases in detectability considering different environmental conditions in different years.

Morphology and population structure.—The characteristics of the individuals from this study are similar to what is known about the species; however, we can highlight some unique findings. The mean SVL we obtained is slightly smaller than that reported by Prival and Schroff (2012), which could be due to the difference in sample size (n = 304 versus n = 24). Sexual dimorphism in *C. pricei* was as expected, with males having longer tails and more subcaudal scales. Prival et al. (2002) pointed out that, in most rattlesnake species, adult males tend to be larger than adult females. That was not the case, however, for *C. pricei* in Aguascalientes. Although males were usually larger than females in T, the mean SVL difference between sexes was not pronounced. This was also confirmed by the SSD index (-0.005), which is consistent with the results of Shine (1994) for the species, although our results must be interpreted with caution given the low number of individuals reported here.

Crotalus pricei specimens from Aguascalientes were not considered in the mitochondrial phylogeny done by Bryson et al. (2011b), and we think that this population is important because it is geographically the closest population of *C. p. pricei* to *C. p. miquihuanus*; therefore, it could bring new insights into the evolutionary history of the species. Bryson et al. (2011b) suggested that the two subspecies of *C. pricei* possibly diverged in the Pleistocene, and that each subspecies contains distinct geographically delineated groups: Northern SMOc (*C. p. pricei*), Southern SMOc (*C. p. pricei*) and Northern SMOr (*C. p. miquihuanus*). Regarding scalation of specimens of *C. pricei* from Aguascalientes, we did not find marked differences compared to other populations of both subspecies of *C. pricei*. The evolutionary history of *C. pricei* is interesting as it is one of the smallest rattlesnakes and may be morphologically and ecologically similar to early rattlesnakes (Prival et al. 2002). In addition, organisms with low vagility are particularly well-suited for studies of speciation because their populations tend to be more exposed to geographic isolation, and as a consequence, this leads to reductions in gene flow and population divergence (Davis et al. 2015; Schield et al. 2018). Further, *C. pricei* is restricted to montane habitats, which are discontinuously distributed across Mexico. Under this scenario of geographic isolation, different populations of the same species became allopatric, and this gene flow break might have led to speciation (Jezkova and Wiens 2018). This lack of gene flow may be why we cannot find similarities among the characteristics of the different groups of *C. pricei* given the biogeographic history of the species. Although they may not represent different species, differences among isolated populations that are also represented in the phylogeny of the group are observable (Bryson et al. 2011b).

There are some characters that help us to differentiate *C. p. pricei* from *C. p. miquihuanus* (Axtell and Sabath 1963; McCranie 1980). *Crotalus p. pricei* tends to have a higher number of VE than *C. p. miquihuanus*, and the female specimens from Aguascalientes overlap with the values reported for *C. p. miquihuanus*; meanwhile, the range in males is similar to *C. p. pricei.* The number of ICS was uninformative, as all values overlapped in all of the groups. The TL:T ratio of our individuals (0.098) is above the known ratio for *C. p. pricei* (0.080; 0.084) and is lower than the reported for *C. p. miquihuanus* (0.114). Axtell and Sabath (1963) mentioned that the TL:T ratio could be the best character to differentiate between *C. pricei* subspecies. Finally, the DS of our specimens were usually fused, and although this is a common pattern for *C. p. miquihuanus*, this characteristic is not conclusive evidence to differentiate between subspecies (Axtell and Sabath 1963). Although this comparison does not define subspecies adscription for the individuals collected in Aguascalientes, they are more similar to *C. p. miquihuanus*, than *C. p. pricei*. Molecular analysis could shed light on this issue in the future.

***Activity patterns and habitat use*.**—We primarily found *C. pricei* in our study area on grassy slopes with leaf litter, and all of them were found near temporary streams. One reason for the association with temporary streams could be that these streams carry and accumulate the leaf litter that the snakes use as shelter. Although the importance of streams (or water bodies in general) for animals is well known, it may have been overlooked for rattlesnakes, although it has been mentioned for other vipers (Roth 2005). In other areas of the SMOc, the presence of *C. pricei* is usually associated with rocky places and occasionally canyon bottoms, but it can also be found in grassy mountain valleys, basking in the open, moving across rocks, or coiled under rocks or vegetation (Armstrong and Murphy 1979; Prival et al. 2002; Bryson et al. 2011a; Grabowsky and Mackessy 2019).

We only found two *C. pricei* individuals in rocky areas despite considerable effort searching in this type of habitat; *C. lepidus* was far more abundant in these rocky habitats. It is therefore important to know the characteristics of the life history of different populations of the same species (Beaupre 1995; Mata-Silva et al. 2018), given that in other parts of its distribution *C. pricei* can be found primarily in rocky habitats (Armstrong and Murphy 1979; Prival et al. 2002). The assumption that the preferences of the species are always the same in all regions can lead to false absences (Shelton et al. 2017; Burns et al. 2019) and increasing difficulty of detecting the species in different habitats in its distributional range (Baxley et al. 2011; Triska et al. 2017). The brief description of the vegetation associated with *C. pricei* presented here increases our understanding of the type of habitat in which the species is found through its southern range of distribution, which is essential to inform management strategies and conservation planning (Degregorio et al. 2011; Burns et al. 2019). Although habitat type concurs with previous studies (Pine-oak Forest), the species and microhabitats vary from what was described by Prival and Schroff (2012). Additionally, most of the snakes that we found were in areas where canopy cover was very low; the highest value that we recorded was 11.8%. This is consistent with the work of Johnson et al. (2016), who indicated that rattlesnakes tend to be more frequent in sites with low levels of canopy cover.

During our field surveys in 2019 and 2020, we were able to find 12 and seven snakes, respectively. Although the conditions in the study site were favorable, these years were the driest in Aguascalientes in the last 5 y (https://smn.conagua.gob.mx/es/climatologia/temperaturas-y-lluvias/resumenes-mensuales-de-temperaturas-y-lluvias). According to Prival and Schroff (2012), the best predictor to account for the detectability of *C. pricei* is the humidity through the year and this could explain the fact that all the snakes were found near temporary streams and leaf litter because these places provide high levels of humidity. Taking this into account, we can assume that in a more humid year in Aguascalientes, we could be able to find even more individuals of *C. pricei*. Therefore, the number of individuals that we found in drier years, compared with previous efforts, could be a good sign for the conservation status of this species in this locality, because species detectability is intimately related to abundance, and it becomes even more important with rare species (Holycross and Goldberg 2001). This prediction, however, should be tested by comparing the abundance of the species in subsequent years. Related to this, Smith et al. (2019) documented that dry years directly affect the population levels of the Copperhead (*Agkistrodon contortrix*) by decreasing the number of offspring that females could bear, hence the importance of continuing to monitor the population of *C. pricei* reported in this study to evaluate their responses to dry and humid years.

Regarding activity patterns, we found 15 of the 19 individuals from July to September. The earliest encounter with *C. pricei* in our study site was after 1000 and the period of time with the most individuals registered was between 1501–1600 (n = 6) followed by 1201–1300 (n = 5). Prival and Schroff (2012) report that these snakes are more active in the summer, mainly after late July, which is consistent with our findings. They also point out that the snakes start basking between 0800–0900, but we did not observe individuals at that time interval. Axtell and Sabath (1963) observed one individual of *C. p. miquihuanus* at 1100 on a sunny day in July 1961, which falls between the intervals in which we were able to find our snakes. There are no reports of nocturnal activity for this species in the literature and we did not detect activity of *C. pricei* during our nocturnal surveys.

Reproduction and behavior.—We recorded one female giving birth to four neonates 12 August 2020, and one female deposited six unfertilized ova 28 August 2020, the later representing the first report of an event like this for *C. pricei*. This is consistent with previous observations: mating occurs generally in August and September and parturition occurs in the summer of the following year with litter size ranging from three to eight neonates (Armstrong and Murphy 1979; Liner and Chaney 1986; Goldberg 2000; Prival and Schroff 2012). Pérez-Mendoza et al. (2018) reported the passing of unfertilized ova for Mexican Dusky Rattlesnake (*C. triseriatus*). As previously mentioned, the snakes that we encountered principally tried to escape among the leaf litter or they would rattle for a few seconds, and this behavior is consistent with the characterization of *C. pricei* being a rather shy rattlesnake (Armstrong and Murphy 1979).

Conservation implications.—In the current biodiversity crisis, we need to understand how species survive in fragmented, marginal, and peripheral populations over long time periods, despite the negative impacts on population size and genetic structure predicted to occur in isolation (Gaston 2000; Burbrink 2010). Therefore, information about the ecology of a given species is crucial to elaborate plans that promote its conservation (Seigel 1986; Prival et al. 2002). The information presented here is important to begin to understand the life-history strategies and conservation requirements of *C. pricei* in the southern extreme of its distributional range. Identifying populations that might be declining or that are at elevated extinction risk allows conservation efforts to be implemented before precipitous declines occur. This type of information is well documented in several vertebrate groups, with the notable exception of reptiles, including most rattlesnakes (Campbell and Flores-Villela 2008; Shelton et al. 2017). In our study area we could observe potential threats to the conservation of this population of *C. pricei,* such as presence of livestock and motorcycle riders. We must also consider the threat represented by the current trend of climate change, which has been documented to affect rattlesnakes inhabiting high altitudes (Davis et al. 2015). Therefore, additional research is needed concerning natural history and evolution of *C. pricei* to allow us to develop appropriate management strategies.

Although the species is protected in Mexico, the population of *C. pricei* inhabiting Aguascalientes indicates that this species may be even more vulnerable than previously thought. It persists in the few remaining patches of high elevation Pine-oak Forests but at low densities, and in specialized niches that might be threatened by climate change. In addition, rattlesnakes are frequently threatened by humans because they are venomous. The information presented in this study represents the first attempt to describe the natural history, morphology, and taxonomic status of the population of *C. pricei* occurring in Aguascalientes. We hope that this information leads to additional natural history studies of this species and that time and funds are spent in monitoring programs.

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