

Diet, size, and pholidosis of *Crotalus ericsmithi*, and new prey items for *Crotalus lannomi* (Serpentes: Viperidae)

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Abstract

Diet, size, and pholidosis of *Crotalus ericsmithi*, and new prey items for *Crotalus lannomi* (Serpentes: Viperidae). *Crotalus ericsmithi* and *Crotalus lannomi* are two of the least studied rattlesnake species endemic to Mexico. We describe the diet and morphological variation of *C. ericsmithi* and report novel prey items for *C. lannomi* based on data from recent field encounters. The diet of *C. ericsmithi* consists mainly of mammals, followed by reptiles, with no detected ontogenetic shift or sexual differences in prey type. This first detailed study of the diet of *C. ericsmithi* adds six new prey species. *Crotalus ericsmithi* does not show sexual dimorphism in snout–vent length and total length, but males have significantly longer tails and smaller head widths and lengths than females. It also exhibits sexual dimorphism in number of subcaudal scales, dorsal body blotches, and tail bands (higher in males), and in midbody dorsal scale rows and intercanthals (higher in females). The mental scale extends posteriorly, preventing contact between the first pair of infralabials in 75% of the specimens examined; therefore, this scale should not be considered a reliable diagnostic character. We identified two new rodent prey items in the diet of wild *C. lannomi*. Our sample sizes are relatively small, reflecting the rarity of these species, so they must be interpreted with caution. Further research into the natural history of the elusive Long-tailed rattlesnakes and their kin are necessary to enhance conservation efforts.

Keywords: Long-tailed Rattlesnake, Mammals, Morphology, Prey, Sexual dimorphism.

Resumo

Dieta, tamanho e folidose de *Crotalus ericsmithi* e novas presas de *Crotalus lannomi* (Serpentes: Viperidae). *Crotalus ericsmithi* e *Crotalus lannomi* são duas das espécies de cascavéis menos estudadas e endêmicas do México. Descrevemos a dieta e a variação morfológica de *C. ericsmithi* e relatamos novos itens de presas para *C. lannomi* com base em dados de recentes

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encontros de campo. A dieta de *C. ericsmithi* consiste principalmente de mamíferos, seguidos por répteis, sem nenhuma mudança ontogenética detectada ou diferenças sexuais no tipo de presa. Este primeiro estudo detalhado da dieta de *C. ericsmithi* acrescenta seis novas espécies de presas. *Crotalus ericsmithi* não apresenta dimorfismo sexual no comprimento focinho-cloaca e comprimento total, mas os machos têm caudas significativamente mais longas e largas e comprimentos de cabeça menores do que as fêmeas. Também exibe dimorfismo sexual no número de escamas subcaudais, manchas dorsais do corpo e faixas da cauda (maior nos machos), e nas fileiras de escamas dorsais do meio do corpo e intercantais (maior nas fêmeas). A escala mental estende-se posteriormente impedindo o contato entre o primeiro par de infralabiais em 75% dos espécimes examinados; portanto, esta escala não deve ser considerada um recurso diagnóstico confiável. Identificamos duas novas presas de roedores na dieta de *C. lannomi* selvagem. O tamanho da nossa amostra é relativamente pequeno, refletindo a raridade destas espécies, por isso devem ser interpretadas com cautela. Defendemos mais pesquisas sobre a história natural das esquivas cascavéis de cauda longa e seus parentes para aumentar os esforços de conservação.

Palavras-chave: Cascavel-de-cauda-longa, Dimorfismo sexual, Mamíferos, Morfologia, Presas.

Introduction

Snakes, particularly venomous species like vipers, are one of the least understood and most persecuted groups of animals. If we add that scarce information is available on the biology of many of these species and that viperids possess “slow” life history traits that make them particularly vulnerable to extinction, face threats such as loss of habitat, mortality caused by humans associated with road traffic, and illegal trafficking of species, we understand why their conservation is a challenge (Maritz *et al.* 2016, Fernández-Badillo *et al.* 2021).

Crotalus ericsmithi Campbell and Flores-Villela, 2008 (Guerreran Long-tailed Rattlesnake), a small and slender-bodied snake endemic to the state of Guerrero, Mexico, is a highly secretive species difficult to find in the field. Since its description, it is known only from a few localities, and the only published information concerns its phylogenetic relationships (Reyes-Velasco *et al.* 2013, Alencar *et al.* 2016, Blair and Sánchez-Ramírez 2016), rattle morphology (Meik and Pires-da-Silva 2009), hemipenial morphology (Jadin *et al.* 2010), and venom composition (Neri-Castro *et al.* 2022). To date, the only information about its natural history is that it can

be active in the early hours of the night and that it occurs in the ecotone between dry pine forest and tropical deciduous forest (Campbell and Flores-Villela 2008). *Crotalus lannomi* Tanner, 1966 (Manantlán Long-tailed Rattlesnake) is another rare rattlesnake reported from the state of Jalisco. Additional specimens were found at two localities in the state of Colima, providing new information about its morphology, activity, behavior, diet, reproduction, and conservation status (Reyes-Velasco *et al.* 2010).

Crotalus ericsmithi and *C. lannomi* plus *C. stejnegeri* Dunn, 1919 (Sinaloa Long-tailed Rattlesnake) are part of the *Crotalus stejnegeri* group and are known as Long-tailed Rattlesnakes. They are rare species endemic to the foothills of western Mexico, occurring from central Sinaloa to central Guerrero, and were recovered as the sister group to the *Crotalus atrox* plus *Crotalus viridis* groups that branched from the *Crotalus durissus* group (Reyes-Velasco *et al.* 2013, Blair and Sanchez-Ramirez 2016), or sister group to the *C. durissus* group (Alencar *et al.* 2016, Holding *et al.* 2021). Although *C. ericsmithi* was not included in the study by Birsakis-Barros *et al.* (2019), it is highly likely that it shares the category of rarest (RT) with its sister species *C. lannomi* and *C. stejnegeri*.

In the case of rare species, growing evidence shows that they play key ecological roles and tend to be more affected by habitat disturbance; therefore, rare vipers are targets of conservation programs (Birskis-Barros *et al.* 2019). Our goal is to contribute to the ecology and conservation of these species by providing information about the diet and morphology of the rare *C. ericsmithi* and to report new data on the diet of *C. lannomi*, based on specimens from recent field surveys.

Materials and Methods

Data Collection

We obtained dietary and morphological data from 21 specimens of *Crotalus ericsmithi*, of which 20 were recently found dead (killed by local residents or road-killed) in the vicinity of the type locality (carretera La Laguna–Bajitos de La Laguna, Guerrero, Mexico; 17.55330° N, 100.77472° W, WGS84; elevation 1037 m a.s.l.), between 2016–2021 and deposited in the herpetological collection of Universidad Autónoma de Aguascalientes (UAAREP-796, 811–827, 981, 1063). We obtained morphological data from the holotype (UTAR-55372) reported by Campbell and Flores-Villela (2008). Snakes were examined for stomach and intestinal contents through a mid-ventral incision.

We obtained scats by palpation of the last third of the body of two *C. lannomi* found 50 km SE from the type locality, which is 2.9 km west of the pass, Puerto Los Mazos, on Mexican Highway 80, Jalisco, Mexico (19.694871° N, 104.414092° W, WGS84; elevation 1151 m a.s.l.) (Reyes-Velasco *et al.* 2010), and released at the same collection site after obtaining morphometric data. A photographic voucher of one *C. lannomi* was deposited at the University of Texas at Arlington (UTADC 9713), and the scat of the second specimen was deposited at Universidad Autónoma de Aguascalientes (UAAREP-1019).

We measured snout–vent length (SVL) and total length (TTL) to the nearest 1 mm with a

measuring tape. Tail length (TL) was obtained by subtracting the SVL from the TTL; head length (HL) and head width (HW) were measured to the nearest 0.1 mm with a digital caliper. We calculated the tail percentage of total length with the following formula $\%TL = TL.100/TTL$. Ontogeny was roughly estimated by examining the rattle structure for near parallelism of successive rattle segments, indicating that growth rates were asymptotic at the time of preservation (Klauber 1940, Meik *et al.* 2010). We determined sex by cloacal probing or by everting hemipenes. We recorded date, locality, number, and identity of prey items. Mass was not included because of the inaccuracy of weight measurements associated with preserved specimens. We calculated the weight ratio (WR) for one *C. ericsmithi* specimen (UAAREP-823) that contained a partially digested prey.

From *Crotalus ericsmithi* we obtained data for 18 pholidosis characters: number of prefrontal scales (PFEN) and number of ventral scales (VEN) following Dowling (1951), subcaudal scales (SBC), midbody dorsal scale rows (MDR), dorsal body blotches (DBB), tail bands (TB), number of intercanthals (ICS), number of supralabial scales (SLS), number of infralabial scales (ILS), number of prefoveal scales (PFO), number of intersupraoculars at midlevel of supraoculars (ISM), presence of mental scale (MEN) produced posteriorly to mostly preclude contact between first pair of infralabials, presence of postrostral scale (PRT), number of internasal scales (INS), number of canthal scales (CAS), number of loreal scales (LOR), presence vs. absence of postloreal scale (PLO), and lacunal–supralabial contact vs. no contact (LAC-SLS) following Campbell and Flores-Villela (2008). For bilateral characters, we usually examined the left side, or the right side only when damage to the specimen prevented us from recording the former. For PRT, PLO, LAC-SLS, we considered it when at least in one side was present. In the results, we present these data as mean \pm one standard deviation.

Identification of Prey Items

Prey remains found in the stomach and intestines of specimens of *Crotalus ericsmithi* and in scats of two *Crotalus lannomi* were stored individually in 70% ethanol. To identify mammal prey, dorsal guard hairs were mounted on glass slides and allowed to set for at least 12 h using a glass coverslip (see Moore *et al.* 1974). These hairs were then compared with those of small mammals (shrews, rodents, skunks, and marsupials) obtained from the mastozoological collection of El Colegio de la Frontera Sur (ECO-SC-M) and from Universidad Autónoma de Aguascalientes (UAA-MA) and with keys to dorsal guard hairs (e.g., Baca-Ibarra and Sánchez-Cordero 2004, Pech-Canché *et al.* 2009). Sometimes, bones, molars, claws, hind limbs, and tails were recovered and used in multiple diagnostics (see Whorley 2000). Reptile scales were identified by comparison with a reference collection of the reptiles from the UAA-REP. Additionally, we used the known distribution of possible prey species as a criterion to reach species-level identification. The data reported for both snakes and their prey follow the suggestions of Maritz *et al.* (2021).

Analyses

Raw morphometric variables of *Crotalus ericsmithi* were tested for normality and homoscedasticity using Shapiro-Wilk and Levene tests. We tested for differences in SVL and TTL of all specimens between sexes using Mann-Whitney U-tests. We calculated the degree of sexual size dimorphism in SVL following Gibbons and Lovich (1990) and Shine (1994). We used Analyses of Covariance (with SVL as the covariate) to detect differences in TL, HL, and HW of all specimens between sexes after we log transformed all variables to meet assumptions of parametric testing, and we tested the assumption of homogeneity of regression slopes. We calculated the WR for only one individual, by dividing the mass of the prey by the mass of

the snake. To detect ontogenetic shift in diet we tested differences between the SVL of snakes and prey taxon using Mann-Whitney U-tests. We performed non-parametric Fisher's Exact Test to compare proportions of specimens containing food items between males and females; the same test was used to compare consumed prey classes (Mammalia and Reptilia) between sexes. We performed Mann-Whitney U-tests for ordinal scale characters, and Fisher's Exact Test for nominal scale characters to compare between sexes and age classes. We performed all statistical analyses in Statistica (StatSoft Inc. 2005), and considered results to be statistically significant when $p \leq 0.05$.

Results

Diet of *Crotalus ericsmithi*

Of the 20 *Crotalus ericsmithi* specimens examined, 12 (60%) contained prey items, for a total of 13 items, 12 in the hindgut, and one in the stomach and hindgut. A total of six prey species were identified; only one specimen contained two types of prey. The class Mammalia represented 84.6%, and class Reptilia represented 15.4% of all samples (Table 1). Regarding mammals, three fecal contents were identified only to Order as unidentified rodents, and one sample to family level as an unidentified Soricidae. In the Order Rodentia and family Cricetidae one individual contained remains of a Deer mouse (*Peromyscus* sp.), and another of a Cotton rat (*Sigmodon* sp.). In the family Heteromyidae, one individual contained remains of the Painted spiny pocket mouse (*Heteromys pictus* Thomas, 1893). In the Order Soricomorpha, family Soricidae, four prey samples represented remains of Goldman's small-eared shrew, *Cryptotis goldmani* (Merriam, 1895). Regarding reptiles, one individual contained remains of a Spiny lizard (*Sceloporus* sp., family Phrynosomatidae), while one individual exhibited cannibalism, containing remains of another *C. ericsmithi* (Table 1). We obtained the weight ratio (WR) of

an adult male *C. ericsmithi* (SVL = 520 mm, TL = 68 mm, TTL = 588 mm, mass = 50 g; UAA-REP 823) that contained a *Peromyscus* sp. (mass = 40 g), yielding a WR = 0.8.

Dietary items were obtained from specimens of SVL 225–550 mm. The SVL of the snakes that fed on mammals ranged from 225–550 mm, mean 379.2 ± 23.2 mm ($N = 10$); snakes that fed on reptiles measured 270–284 mm, mean 277 ± 9.9 mm ($N = 2$). No differences in SVL were found between the snakes that consumed mammals or reptiles ($Z = 1.07$, $p = 0.28$; $N_{\text{juveniles}} = 8$, $N_{\text{adults}} = 4$; Figure 1), implying no appreciable ontogenetic shift, although our sample size is small. Males (60% of $N = 10$) and females (60% of $N = 10$) were equally likely to contain prey items (Fisher's Exact Test, $p = 0.67$). There was no significant difference in prey class (Mammalia and Reptilia) consumed between sexes (Fisher's Exact Test, $p = 0.77$).

Size and Pholidosis of *Crotalus ericsmithi*

The largest male in our sample measured 588 mm TTL (SVL = 520 mm, TL = 68 mm; UAAREP-823), the largest female 689 mm TTL (SVL = 625 mm, TL = 64 mm; UAAREP-822). Snout–vent length of all specimens ranged between 225–625 mm (394.9 ± 118.7 ; $N = 21$) and TTL between 251–689 mm (446 ± 136.2 ; $N = 21$). SVL of juveniles ranged between 225–364 mm (293.8 ± 42.1 ; $N = 11$) and TTL between 251–419 mm (328 ± 50.8 ; $N = 11$). SVL of adults ranged between 450–625 mm (506 ± 56.1 ; $N = 10$) and TTL between 521–689 mm (575.9 ± 50.9 ; $N = 10$). SVL of males (400.8 ± 85.5 ; $N = 11$) was 3.11% larger than that of females (388.3 ± 152 ; $N = 10$), and did not vary significantly ($Z = 0.49$, $p = 0.62$). The degree of sexual size dimorphism in SVL of all specimens was -0.03 . We found no significant difference in TTL ($Z = 0.56$, $p = 0.57$), between males (460.9 ± 103.6 ; $N = 11$) and females (429.7 ± 169.5 ; $N = 10$), but males were generally longer. The TL of juvenile males ranged between 33–55 mm (41.6 ± 9.8 ; $N = 5$) and juvenile females between 23–34 mm

Table 1. Frequency and percentage of occurrence of the taxa that comprise the diet of *Crotalus ericsmithi* from specimens analyzed in this study.

Prey taxon	Frequency	%
MAMMALIA	11	84.6
SORICOMORPHA		
Soricidae		
Unidentified shrew	1	7.7
<i>Cryptotis goldmani</i>	4	30.8
RODENTIA		
Unidentified rodent	3	23
Cricetidae		
<i>Peromyscus</i> sp.	1	7.7
<i>Sigmodon</i> sp.	1	7.7
Heteromyidae		
<i>Heteromys pictus</i>	1	7.7
REPTILIA	2	15.4
SQUAMATA		
Phrynosomatidae		
<i>Sceloporus</i> sp.	1	7.7
Viperidae		
<i>Crotalus ericsmithi</i>	1	7.7
Total	13	100

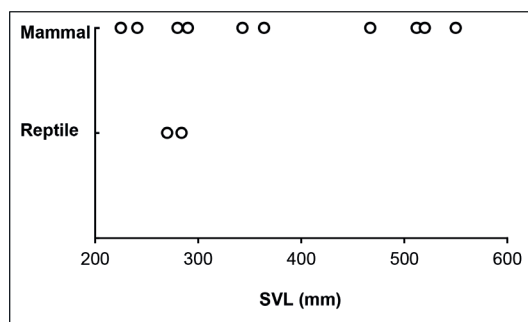


Figure 1. Relationship between prey types (mammals and reptiles) and snake snout–vent length (SVL) of individuals of *Crotalus ericsmithi*.

(28 ± 3.8; N = 6). TL of adult males ranged between 68–86 mm (75.5 ± 6.3; N = 6) and adult females between 54–73 mm (61.5 ± 8.9; N = 4). The TL of males (60.1 ± 19.3 mm; 13% of TTL; N = 11) was longer than that of females (41.4 ± 18.3 mm; 9.6% of TTL; N = 10) of all specimens, as was the %TL of males (Table 2). Females had significantly shorter tails than males ($F_{2,18} = 250.79, p < 0.0001$).

The HL of juvenile males ranged between 17–21.4 mm (19.3 ± 1.9; N = 5) and juvenile females between 16–21 mm (18 ± 1.8; N = 6). HL of adult males ranged between 23–27 mm

(25.5 ± 1.9; N = 6) and adult females between 28–33 (30.5 ± 2.4; N = 4). We found significant difference between female HL (N = 10) and males HL (N = 11) of all specimens ($F_{2,18} = 208.68, p = 0.0001$), with females having longer heads (Table 2). The HW of juvenile males ranged between 8–13.1 mm (11 ± 2.4; N = 5) and juvenile females between 8–13 mm (10.2 ± 2.3; N = 5). HW of adult males ranged between 13.5–14.8 mm (13.8 ± 0.8; N = 6) and adult females between 17–24 mm (19 ± 3.4; N = 4). We found significant difference between female HW (N = 9) and males HW (N = 11) of all

Table 2. Sample sizes (N), mean (± standard deviation), and range of snout-vent length (SVL, mm), tail length (TL, mm), percentage of tail length (%TL), total length (TTL, mm), head length (HL, mm), head width (HW, mm), and scale counts of prefrontals (PVEN), ventrals (VEN), subcaudals (SBC), midbody dorsal scale rows (MDR), dorsal body blotches (DBB), tail bands (TB), intercanthals (ICS), supralabials (SLS), infralabials (ILS), prefoveal (PFO) and intersupraoculars at midlevel of supraoculars (ISM) of both sexes of *Crotalus ericsmithi* analyzed in this study.

	Males			Females		
	N	Mean ± SD	Range	N	Mean ± SD	Range
SVL	11	400.8 ± 85.5	284–520	10	388.3 ± 152	754–1519
TL	11	60.1 ± 19.3	33–86	10	41.4 ± 18.3	23–73
%TL	11	12.8 ± 1.8	10.4–15.9	10	9.5 ± 1.0	7.8–11.8
TTL	11	460.9 ± 103.6	317–588	10	429.7 ± 169.5	251–689
HL	11	22.5 ± 3.5	17–27	10	23.0 ± 6.7	16–33
HW	11	12.6 ± 2.2	8–14.8	10	14.1 ± 5.3	8–24
PVEN	11	2.7 ± 0.5	2–3	10	2.8 ± 0.8	3–4
VEN	11	174.0 ± 2.4	172–179	10	173.6 ± 3.0	169–180
SBC	11	42.7 ± 1.3	41–45	10	34.3 ± 0.9	33–36
MDR	11	25.5 ± 0.8	25–27	10	26.8 ± 1.4	25–29
DBB	11	37.5 ± 2.3	34–41	10	35.3 ± 1.3	33–37
TB	11	14.5 ± 2.1	12–18	10	12.3 ± 1.9	10–16
ICS	10	1.7 ± 1.1	1–4	10	3.4 ± 1.3	2–6
SLS	10	13.4 ± 0.7	12–14	9	14.0 ± 0.5	13–15
ILS	10	14.5 ± 0.5	14–15	10	14.8 ± 0.6	14–16
PFO	10	4.7 ± 0.9	3–6	9	4.9 ± 1.1	4–6
ISM	10	4.6 ± 0.5	4–5	10	4.5 ± 0.7	3–5

specimens ($F_{2,1} = 44.25$, $p = 0.0001$) with females having wider heads.

MEN was present in 15 of 20 *Crotalus ericsmithi* (75%). In the five specimens where the first supralabials are in partial contact, the mental scale is similar to the shape of that of *C. lannomi* (Figure 2). No significant differences were found between sexes ($N_{\text{males}} = 8$ of 10; $N_{\text{females}} = 7$ of 10; Fisher's Exact Test, $p = 0.5$) and age classes ($N_{\text{juveniles}} = 7$ of 10; $N_{\text{adults}} = 8$ of 10; Fisher's Exact Test, $p = 0.5$), when comparing the presence of MEN. The postrostral scale (PRT) was absent in all specimens, INS was paired in all specimens, except one having one internasal on the left side and two on the right side, and CAS was paired in all specimens. We found two loreal scales (LOR) (one upper and one lower loreal) on each side in all specimens. The lacunal-supralabial (LAC-SLS) contact was absent in all specimens, except in one on the left side of the head.

Males were significantly different from females in SBC ($Z = 3.87$, $p < 0.0001$), DBB (Z

$= 2.25$, $p = 0.02$), TB ($Z = 2.35$, $p = 0.01$) being higher in males, and in MDR ($Z = -2.0$, $p = 0.04$), which was higher in females. We found no significant differences between sexes in PVEN ($Z = -0.07$, $p = 0.94$), VEN ($Z = 0.14$, $p = 0.88$), ISM ($Z = 0.15$, $p = 0.87$), PFO ($Z = -0.28$, $p = 0.77$), SLS ($Z = -1.67$, $p = 0.09$) or ILS ($Z = -0.94$, $p = 0.34$; Table 2). The number of ICS varies significantly ($Z = -2.68$, $p = 0.007$) between males (1–2 scales anteriorly and 0–2 scales posteriorly) and females (0–3 scales anteriorly and 1–3 posteriorly), being higher in females. We found no significant differences between sexes in the presence of PLO ($N_{\text{males}} = 5$ of 10; $N_{\text{females}} = 8$ of 10; Fisher's Exact Test, $p = 0.17$; present in 65% of all specimens, $N = 20$).

Diet of Crotalus lannomi

Two scats of *Crotalus lannomi* were obtained. The scat obtained from an adult female *C. lannomi* (SVL = 470 mm, TL = 50 mm, TTL = 520 mm; UTADC 9713) contained hairs and

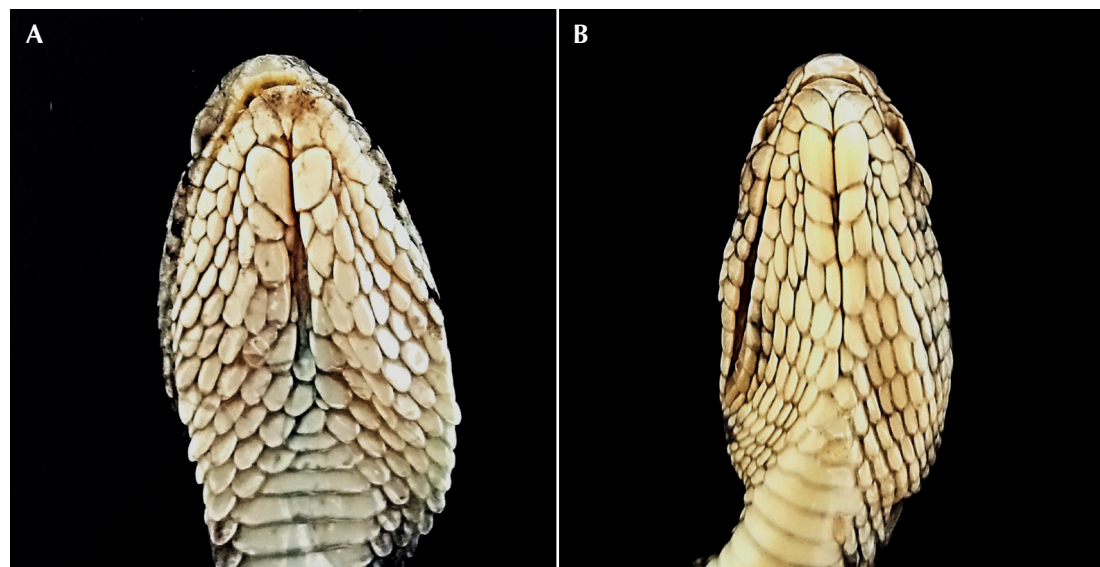


Figure 2. (A) Adult female *Crotalus ericsmithi* (UAAREP-827) with the first pair of infralabials mostly separated by the mental. (B) Adult male *Crotalus ericsmithi* (UAAREP-823) with mental produced anteriorly and the first pair of infralabials in broad contact.

molars that were identified as a Cotton Rat (*Sigmodon* sp.). The scat of a juvenile male (SVL = 320 mm, TL = 44 mm, TTL = 364 mm, HL = 21 mm; UAA-REP 1019) also contained remains of a Cotton Rat (*Sigmodon* sp.), as well as remains of insects; the latter are usually considered secondary ingestion.

Discussion

Diet Variation in Crotalus ericsmithi

Due to the scarcity of information about *Crotalus ericsmithi*, any documented prey has value. Furthermore, little is known about its biology, natural history, and morphology (Campbell and Flores-Villela 2008, Meik and Pires-da-Silva 2009, Jadin *et al.* 2010). For natural history, the related species *C. stejnegeri* can exhibit arboreal behavior (Van Der Heiden 2021, Aguirre-Zazueta *et al.* 2022), although it is not known for what purpose they climb vegetation (e.g., thermoregulation, foraging, or to avoid predation). It is likely that this behavior is also present in *C. lannomi* and *C. ericsmithi*. Diet information for *C. lannomi* and *C. stejnegeri* is scarce (Klauber 1972, Reyes-Velasco *et al.* 2010, Aguirre-Zazueta *et al.* 2022).

Our results revealed that *Crotalus ericsmithi* most likely specializes in consuming mammalian prey (84.6%) and to a lesser extent, reptiles. Among mammals, the main prey were shrews [*Cryptotis goldmani* (Merriam, 1895) and an unidentified shrew], followed by rodents, *Peromyscus* sp., *Sigmodon* sp., and *H. pictus*. The frequent consumption of shrews may be because they are small and easy to swallow and are abundant in pine-oak forest, the type of vegetation occurring in the area inhabited by *C. ericsmithi*. Rodents in the family Cricetidae reported in this study correspond to findings for *C. lannomi* and *C. stejnegeri* (Klauber 1972, Aguirre-Zazueta *et al.* 2022). More information on the diet of *C. lannomi* and *C. stejnegeri* and an increase the number of samples for *C. ericsmithi* will allow a better comparison of diet among these species.

Specialization on mammals by *Crotalus ericsmithi* coincides with a similar mammal diet of related species like *Crotalus horridus* Linnaeus, 1758 (Timber Rattlesnake) (Clark 2002, Reinert *et al.* 2011), as well as in members of the *C. durissus* group, such as *Crotalus durissus* Linnaeus, 1758 (Neotropical Rattlesnake) (Salomão *et al.* 1995, Sant'Anna and Abe 2007, Hoyos and Almeida-Santos 2016), *Crotalus tzabcan* Klauber, 1952 (Tzabcan Rattlesnake) (Carbajal-Márquez *et al.* 2020a), the *C. atrox* group, such as *Crotalus atrox* Baird and Girard, 1853 (Western Diamond-backed Rattlesnake) (Reynolds and Scott 1982, Pisani and Stephenson 1991, Spencer 2003), and *Crotalus ruber* Cope, 1892 (Red Diamond Rattlesnake) (Dugan and Hayes 2012).

Reptiles accounted for 15.4% of prey items in the diet of *C. ericsmithi*. A Spiny Lizard (*Sceloporus* sp.) and a snake (*C. ericsmithi*) were consumed by newborn specimens. Rattlesnake species closely related to *C. ericsmithi*, such as *C. lannomi*, are known to consume reptiles (Reyes-Velasco *et al.* 2010); however, related medium- to large-bodied species with large young consume mainly mammals from birth but rarely consume reptiles (Clark 2002, Spencer 2003, Reinert *et al.* 2011, Hoyos and Almeida-Santos 2016). Lizards are common prey of newborn and juvenile small-bodied rattlesnakes, although they may also be consumed by adults (Keenlyne and Beer 1973, Campbell and Armstrong 1979, Holycross *et al.* 2002, Prival and Schroff 2012, Güizado-Rodríguez *et al.* 2016, Mociño-Deloya 2016).

It is not surprising that a hatchling of *Crotalus ericsmithi* fed on a conspecific individual. Members of the *C. stejnegeri* group consume other snakes (Reyes-Velasco *et al.* 2010). Cannibalism has been reported in wild, mostly adult individuals of *Crotalus aquilus* Klauber, 1952 (Queretaran Dusky Rattlesnake) (Mociño-Deloya 2016), *C. atrox* (Myers 2015), *C. cerastes* Hallowell, 1854 (Sidewinder) (Funk 1965), *C. triseriatus* Wagler, 1830 (Western Dusky Rattlesnake) (Mociño-Deloya and Setser 2009),

C. polystictus (Cope, 1865) (Mexican Lancehead Rattlesnake) (Mociño-Deloya *et al.* 2009, Mociño-Deloya 2016), *C. pricei* Van Denburgh, 1895 (Twin Spotted Rattlesnake) (Prival and Schroff 2012), *C. viridis* (Rafinesque, 1818) (Prairie Rattlesnake) (Gloyd 1933, Genter 1984), and *Sistrurus catenatus* (Rafinesque, 1818) (Massasauga) (Ruthven 1911, Hallock 1991).

Juveniles of *Crotalus ericsmithi* feed on both mammals and reptiles, and adults apparently only mammals. We did not find significant differences between the size of the snakes regarding the type of prey consumed, indicating that *C. ericsmithi* feeds on mammals at all stages of life, although the sample size is small. Because of the advanced degree of digestion of prey recovered from specimens of *C. ericsmithi*, we could not obtain the size of most prey. The WR estimated for adult male *C. ericsmithi* and its *Peromyscus* sp. prey was fairly high and is a consistent pattern for vipers, since they occasionally consume large prey with a high WR, even higher than WR = 1.0 (Greene 1983, 1992, Loughran *et al.* 2013).

Size and Pholidosis Variation of *Crotalus ericsmithi*

Males and females of *Crotalus ericsmithi* have are similar in body size. With the few data available, it appears that *C. lannomi* (SVL = 569 mm, TTL = 638 mm; Reyes-Velasco *et al.* 2010) is similar in size as *C. ericsmithi*, and *C. stejnegeri* is longer (TTL = 790 mm; Van Der Heiden and Flores-Villela 2013). Both species appear to have males and females of similar sizes. Although *C. durissus* and *C. tzabcan* do not show sexual dimorphism in SVL and TTL (Santa'Anna and Abe 2007, Barros *et al.* 2012, Carbajal-Márquez *et al.* 2020a,b), dimorphism occurs in other related species as *C. horridus* (Gibbons 1972), *C. atrox* (Spencer 2003), *C. catalinensis* Cliff, 1954 (Avila-Villegas *et al.* 2007), and *C. ruber* (Dugan and Hayes 2012).

Crotalus ericsmithi is sexually dimorphic in TL (males have longer tails). The greater %TL

in males of *C. ericsmithi* is similar to the greater %TL reported for males of *C. lannomi* (Reyes-Velasco *et al.* 2010) and *C. stejnegeri* (Van Der Heiden and Flores-Villela 2013). The maximum %TL reached by *C. ericsmithi* (15.9%) is greater than that reported for *C. lannomi* (14.4%) and *C. stejnegeri* (14.5%). The related species *C. durissus* and *C. tzabcan* are sexually dimorphic in TL, and due to the presence of hemipenes, most rattlesnakes are sexually dimorphic (Barros *et al.* 2012, Carbajal-Márquez *et al.* 2020a,b).

The smaller HL and HW in males of *Crotalus ericsmithi* suggest that sexual differences may influence the size of prey they consume; however, we could not determine the size of most prey, and we found no sex differences in the prey classes consumed. Although SVL is not significantly different between sexes, females have greater HL and HW and may possibly feed on larger prey items. Forsman and Lindell (1993) found that swallowing performance varied among snakes of the same SVL because of differences in HL. Sexual differences in HL and HW may also be due to phenotypic plasticity in response to environmental factors (Meik *et al.* 2012). Data to compare HL and HW in the closely related species *C. lannomi* and *C. stejnegeri* is insufficient (Reyes-Velasco *et al.* 2010, Van Der Heiden and Flores-Villela 2013). Other species related to *C. ericsmithi* show no sex differences in prey type consumed as *C. atrox* (Spencer 2003), *C. catalinensis* (Avila-Villegas *et al.* 2007), *C. durissus* (Santa'Anna and Abe 2007), *C. horridus* (Reinert *et al.* 2011, Wittenberg 2012), prey mass as *C. ruber* (Dugan and Hayes 2012), or prey type and mass in *C. tzabcan* (Carbajal-Márquez *et al.* 2020a).

MEN was present in 75% of specimens of *Crotalus ericsmithi*. This separation is apparently not dependent on sex or age. The shape of the mental scale in the five specimens examined does not prevent contact of the first supralabials and is similar to the shape in *C. lannomi* (Campbell and Flores-Villela 2008). This character is not reliably diagnostic.

Crotalus ericsmithi is sexually dimorphic in MDR and ICS (greater number in females). Because of the small number of specimens, no data are available to verify if this pattern is shared with *C. lannomi* (MDR = 25–29; ICS male = 0–4; ICS female = 2–3) and *C. stejnegeri* (MDR = 25–27; ICS = 2–12) (Reyes-Velasco et al. 2010, Van Der Heiden and Flores-Villela 2013). *C. ericsmithi* is sexually dimorphic in SBC, DBB, and TB (greater number in males). This trend is apparently present in *C. lannomi* SBC (male = 49; female = 35–37), *C. stejnegeri* SBC (male = 42–45; female = 36–37) and *C. lannomi* DBB (male = 35; female = 31–33) but not in *C. stejnegeri* DBB (male = 32–43; female = 34–43). Sexual dimorphism is apparently present in *C. lannomi* TB (male = 12–17; female = 12–15), but data are insufficient for *C. stejnegeri* TB (13–16).

Sexual dimorphism was not significant in other characters of pholidosis of *Crotalus ericsmithi*, similar to *C. lannomi* VEN (male = 171–175; female = 168–176) and *C. stejnegeri* VEN (male = 172–178; female = 171–176), where the number of VEN overlap between sexes (Reyes-Velasco et al. 2010, Van Der Heiden and Flores-Villela 2013). The paired INS found in all specimens of *C. ericsmithi* (except for one specimen with one internasal on the left side and two on the right side) is comparable to *C. lannomi*, which has relatively narrow and commonly paired INS, except for two specimens that have two internasals on the left side and one on the right side (UTADC 4003, 4006; see Reyes-Velasco et al. 2010). *Crotalus stejnegeri* has broad triangular and commonly paired INS (Van Der Heiden and Flores-Villela 2013). The absence of sexual differences in ISM seems to be present in *C. lannomi* (male = 3–4; female = 4–5) and *C. stejnegeri* (5–8). Data are insufficient to compare *C. lannomi* PFO (4) and *C. stejnegeri* PFO (7–8) (Campbell and Lamar 2004, Reyes-Velasco et al. 2010, Van Der Heiden and Flores-Villela 2013).

Crotalus ericsmithi is a slender rattlesnake that is not sexually dimorphic in body length. Females of *C. ericsmithi* have a greater number

of MDR, possibly because increased maternal body size allows larger clutches (Shine 2000). Greater MDR in females may also be related to their larger HL and HW, allowing them to consume larger prey items, thus sequestering more energy available for growth, storage, and reproduction (Forsman and Lindell 1993, Shine 2000). This greater girth in females is also present in *C. lannomi* (Reyes-Velasco et al. 2010). Additionally, the greater number of ICS in females may be related to a larger HL and HW than in males. The greater number of SBC and TB in males has been previously reported for *C. stejnegeri* and for related species such as *C. durissus*, *C. tzabcan*, and most species in the genus, possibly because of the presence of the hemipenes (Klauber 1952, Campbell and Lamar, 2004, Carbajal-Márquez et al. 2020b).


Diet of *Crotalus lannomi*

Both prey items of *Crotalus lannomi* obtained in this study are mammals. Only two diet records, both mammals, are known for *C. stejnegeri* (Klauber 1972, Aguirre-Zazueta et al. 2022). Reyes-Velasco et al. (2010) observed that a juvenile specimen of *C. lannomi* found in July 2008 contained scales from a lizard (*Sceloporus* sp.), arthropod remains, plant matter, and an unidentified snake jaw. It is likely that *C. lannomi* and *C. stejnegeri* have feeding habits similar to *C. ericsmithi*, which may be a shared pattern in Long-tailed rattlesnakes.

Our study provides baseline data on the diet and morphology of specimens of wild *Crotalus ericsmithi*, and adds new diet data for *C. lannomi*. Both species are secretive and difficult to encounter and study in the field; thus, any new information is valuable. *Crotalus ericsmithi* is likely a specialized mammal predator, with habits similar to its related species, members of the *C. atrox* and *C. durissus* groups. Our sample size is relatively small and must be interpreted with caution, but it reflects the difficulty of accessing areas where these rattlesnakes live, the rarity of the species, the difficulty of finding

specimens that have recently eaten, and the infrequent collection of individuals. Snakes face several threats to their survival (e.g., climate change, habitat loss, illegal species trafficking; see Fernández-Badillo *et al.* 2021). The diet and morphological data provided here contribute to our understanding of the biology and ecology of *C. ericsmithi* and *C. lannomi*, and how these data relate to that of other rattlesnakes, leading to better decision-making regarding conservation. Additional data must be collected to further our knowledge of the natural history and distribution of these enigmatic rattlesnakes.

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