Life History, Activity Pattern, and Morphology of *Crotalus tzabcan* Klauber, 1952 (Serpentes: Viperidae)

Rubén Alonso Carbajal-Márquez[1,2], J. Rogelio Cedeño-Vázquez[1,5], Marcio Martins[3], and Gunther Köhler[4]

[1]*El Colegio de la Frontera Sur, Departamento de Sistemática y Ecología Acuática, Unidad Chetumal, Avenida Centenario Km 5.5, 77014, Chetumal, Quintana Roo, México*
[2]*Conservación de la Biodiversidad del Centro de México, Asociación Civil, Andador Torre de Marfil No. 100, 20229, Aguascalientes, Aguascalientes, México*
[3]*Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, 05508-090 São Paulo, São Paulo, Brasil*
[4]*Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany*
[5]*Corresponding author, e-mail: rogeliocedeno@gmail.com, rcedenov@ecosur.mx*

Abstract.—The Tzabcan Rattlesnake (*Crotalus tzabcan*) is a highly secretive species that is difficult to observe and follow in the field and any information that can be generated is essential to gain a better understanding of its biology and ecology. *Crotalus tzabcan* is a large and heavy-bodied species, with a maximum snout-vent length of 1,667 mm and a total length of 1,818 mm. It is endemic to the Yucatán Peninsula, and very little is known about its natural history. We provide data on life history, activity, and morphology based on specimens that we obtained in recent field surveys, museums, and anecdotal observations. *Crotalus tzabcan* does not present sexual dimorphism in snout-vent length or total length, but males have heads and tails that are significantly longer than females. We observed an ontogenetic color change, where newborns and juveniles had a darker base color and blotches than adults. *Crotalus tzabcan* showed a unimodal activity pattern with peak activity in the summer. We observed crepuscular and nocturnal activity during the warmer months and diurnal activity during the cooler months. The timing of *C. tzabcan* reproductive events, based on behavioral evidence and activity, is similar to other pitvipers and rattlesnakes from temperate and tropical zones. We encourage additional research on behavior, physiology, histology, and on how environmental conditions influence life-history traits, to determine the reproductive cycle in both sexes more accurately, which could subsidize conservation strategies.

Key Words.—mating; ontogenetic color change; rattlesnake; sexual dimorphism; unimodal activity pattern; Yucatán Peninsula

Introduction

The Tzabcan Rattlesnake (*Crotalus tzabcan* Klauber, 1952), a large and heavy-bodied snake endemic to the Yucatán Peninsula, is a highly secretive species difficult to observe and follow in the field. Despite its relatively wide distribution, previous studies have only addressed morphology, and information on the life history of this species and its activity in the wild is scarce (Klauber 1952; Armstrong and Murphy 1979; Lee 1996). *Crotalus tzabcan* is listed in the Red List of the International Union for the Conservation of Nature (IUCN) as Least Concern (Acevedo et al. 2014) and is not considered to be endangered in Mexico (Secretaría de Medio Ambiente y Recursos Naturales, México [SEMARNAT] 2010). Yet it is Highly Vulnerable according to the Environmental Vulnerability Score (Wilson et al. 2013) and occupies the 12th position of the ecological and evolutionary distinctiveness index for conservation prioritization of world vipers (Maritz et al. 2016). Factors like habitat loss, disease, or the presence of introduced species can cause a species to become threatened. Life-history traits (e.g., time of juvenile recruitment, size at birth, and sexual dimorphism), however, play an important role in determining the sensitivity or resilience of species to these stressors and constitute the raw data for building the population models used in extinction risk assessments and management programs of endangered species (IUCN 2001; Lindenmayer and Burgman 2005). Understanding life-history traits is therefore critical for species conservation. Our goal in this study was to provide information about the life history, activity patterns, and morphology of *C. tzabcan,* based on specimens that we obtained in recent field surveys, museums, and isolated observations, which serve as a baseline for future studies on the ecology and conservation of *Crotalus tzabcan*.

Materials and Methods

Study area.—We conducted this study at different locations across the Yucatán Peninsula (in the

states of Campeche, Quintana Roo, and Yucatán) in Mexico. This region is a calcareous platform with great heterogeneity in its geological gradients, and a combination of geomorphological, climatological, hydrological, edaphic, and ecological factors promoted the development of a particular type of biodiversity, resulting in a distinctive biogeographical unit (Torrescano-Valle and Folan 2015). Warm and relatively homogeneous temperatures throughout the year (averages between 25.5–26.7° C) are characteristic of the climate in this region. There is a prolonged dry season from November to April (< 60 mm of rainfall per month), a wet season from May to October (> 60 mm of rainfall per month), and between December and February there are occasional winter rainfalls due to cold fronts. The main types of vegetation are low deciduous forests, low semi-deciduous forests with columnar cacti, low and medium semideciduous forests, high, medium, and low semi-evergreen forests, high evergreen forest, savannas, palm groves, mangroves, coastal dunes, marshes, tulles, and reed beds (Vidal-Zepeda 2005; Torrescano-Valle and Folan 2015).

Field methods.—We conducted monthly field surveys for 5–15 d, from January to December 2015. We selected sampling sites based on collections reported in the literature (Lee 1996) and those in electronic databases with the highest concentration of historical records (Global Biodiversity Information Facility. 2018. GBIF, biodiversity data. Available from http://www.gbif.org. [Accessed 8 January 2015]; National Science Foundation. 2018. VertNet. Version 2016-09-29. Available from http://www.vertnet.org. [Accessed 10 January 2015]). A minimum of two people performed visual encounter surveys by day (0800–1100) and at night (1800–2200). We also carried out road surveys close to the visual survey sites to search for snakes at night (1930–0000). We conducted additional opportunistic road surveys, without calculating the sampling effort, throughout 2016–2017 in areas surrounding Chetumal, Quintana Roo, Mexico.

We captured rattlesnakes using tongs and tubes, then we recorded the time, date, coordinates, and location of each capture. For every snake, we measured the snout-vent length (SVL; ± 1 mm) and tail length (TL; ± 1 mm) with a measuring tape and head length (HL; ± 1 mm) with a digital caliper. We used only HL measures because they varied less than head width when dealing with road-killed snakes. We determined sex by cloacal probing or by everting hemipenes. We palpated females to detect embryos or enlarged follicles. To evaluate the ontogenetic change in color, we considered only live or freshly killed specimens and two pattern categories (approximated with a binary scale, dark versus light color), and excluded all preserved specimens due to loss of original pigmentation.

Additionally, we obtained data for 14 morphological characters: number of ventral scales (VEN), subcaudal scales (SBC), midbody dorsal scale rows (MDR), midtail dorsal scale rows (MTR), dorsal body blotches (DBB), bands on the tail (TLB), number of scales widthwise on the paravertebral stripes (transverse count; WPS), number of scales lengthwise on the paravertebral stripes (longitudinal count; LPS), number of supralabial scales (SLS), number of infralabial scales (ILS), presence of intercanthals (ICS), presence versus absence of a divided first infralabial scale (DFI), presence versus absence of the postrostral scale (PRT), and presence versus absence of contact between the prenasal and the first supralabial scale (PRE-SLS). In the results, we present these data as mean ± one standard deviation. We processed live snakes *in situ* and released them immediately after gathering data. We stored road-killed specimens and those killed by local people in 70% ethanol and deposited them in the herpetological collection of El Colegio de la Frontera Sur (ECO-CH-H) in Chetumal, Quintana Roo, Mexico. We also checked 30 specimens (with complete collection data) that others deposited in the ECO-CH-H collection from 1992–2013. Additionally, we included anecdotal behavioral observations of *C. tzabcan* that we obtained during visual encounter and road surveys.

Analyses.—We used all the specimens available to us (live, freshly road-killed, and museum specimens) and considered the capture frequency to be an indicator of general activity. Herein, general activity corresponds to any animal activity on a substrate surface (e.g., basking, foraging, searching for mates) that increased the probability of encounter. Variables were normal (Kolmogorov-Smirnov test) and homoscedastic (Levene test). We tested for differences in SVL and total length (TTL) between adults of both sexes with the Student *t*-test for normal data. 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 relative tail length (RTL) and relative head length (RHL) between ages and sexes after we log transformed all variables to meet assumptions of parametric testing, and we tested the assumption of homogeneity of regression slopes. We performed Mann-Whitney U-tests for ordinal scale characters, and Fisher´s Exact Test for nominal scale characters to compare males and females.

We delimited the seasons of the year based on the equinoctial and solstitial periods in the Northern Hemisphere: Spring (21 March to 21 June), Summer (22 June to 22 September), Autumn (23 September to 21 December), and Winter (22 December to 20 March). We used Fisher´s Exact Test to evaluate capture frequency differences in age classes and sexes among

TABLE 1. Sample sizes (n), mean (± standard deviation), and range (below means) of snout-vent length (SVL, mm), tail length (TL, mm), relative tail length (RTL, % of SVL), total length (TTL, mm), head length (HL, mm), and relative head length (RHL, % of SVL) of newborn, juvenile, and adult Tzabcan Rattlesnake (*Crotalus tzabcan*) specimens found during 2015–2017 in the Yucatán Peninsula, and specimens from the Herpetological Collection of El Colegio de la Frontera Sur (ECO-CH-H). Abbreviations are: NM = newborn male, NF = newborn female, JM = juvenile male, JF = juvenile female, AM = adult male, AF = adult female.

	NM	NF	JM	JF	AM	AF
n	10	5	10	5	14	8
SVL	328.9 ± 41.6	331.6 ± 29.6	523.1 ± 106.3	482.6 ± 62.7	1245.3 ± 277.1	1340 ± 125.5
	255–388	292–361	410–676	415–550	743–1667	1100–1515
TL	34.2 ± 4	29 ± 5.8	51 ± 10.4	38.8 ± 6.2	128 ± 31.1	98.2 ± 4.7
	28–38	24–38	41–66	31–47	75–168	90–104
RTL	10.4 ± 1.3	8.8 ± 2.3	9.7 ± 0.3	8 ± 0.7	10.2 ± 0.8	10.2 ± 0.8
	8.2–12.8	7.2–13	9.2–10.2	7.2–8.9	9–11.5	6.9–8.1
TTL	363.1 ± 43.6	360.6 ± 28.1	574.1 ± 116.7	521.4 ± 67.8	1373.4 ± 306.7	1438.2 ± 129.5
	285–426	330–391	452–741	451–593	818–1818	1190–1619
HL	25.5 ± 3.8	23.8 ± 2.3	33.3 ± 4.0	29 ± 3.9	55.7 ± 7.7	54.5 ± 5.6
	20–32	20–26	28–40	23–33	40–67	45–60
RHL	7.7 ± 0.8	7.1 ± 0.3	6.2 ± 0.5	6.1 ± 0.6	4.6 ± 0.5	4.0 ± 0.3
	6.8–9.3	6.8–7.5	5.4–7.0	5.5–7.2	4.1–5.4	3.8–4.5

seasons. For all these analyses, we considered an adult to be an individual with a TTL ≥ 800 mm (based on the minimum reproductive size of the closely related South American Rattlesnake, *C. durissus*; Almeida-Santos et al. 2004a,b; Barros et al. 2012), a newborn to be an individual with only a prebutton, a single button or a button with a second rattle (Klauber 1940), and a juvenile to be an individual with a TTL < 800 mm and with more than two buttons on the rattle. We performed all statistical analyses in Statistica (StatSoft Inc., Tulsa, Oklahoma, USA), and considered results to be statistically significant when $P \leq 0.05$.

RESULTS

We examined 52 specimens, of which 22 were live individuals or freshly road-killed (January 2015 to February 2017) and 30 were from the ECO-CH-H collection (September 1992 to August 2013). During our visual encounter surveys (sampling effort: 390.5 search-hours), we only found two live rattlesnakes (encounter rate: one snake per 195.2 search-hours). During the nocturnal road surveys in 2015, we only found four freshly road-killed rattlesnakes (sampling effort: 4,913.6 km; encounter rate: one snake per 1,228.4 km). We found the remaining 16 specimens (two live and 14 freshly road-killed) during nocturnal road surveys in the outskirts of Chetumal, without recording the sampling effort.

The largest male in our sample measured 1,818 mm TTL (SVL = 1,667 mm, TL = 151 mm), and the largest female, 1,619 mm TTL (SVL = 1,515 mm, TL = 104 mm). The SVL of *C. tzabcan* adult males and females was not significantly different ($t = -0.901$, df = 20, $P = 0.373$), although females were generally slightly larger (Table 1). The degree of sexual size dimorphism in

SVL was 0.07. We found no significant difference in TTL between sexes ($t = -0.564$, df = 20, $P = 0.777$), but adult females were generally longer. Adult females had significantly shorter tails (RTL) than adult males ($F_{1,20} = 83.62$, $P < 0.001$). Adult female heads (RHL) were significantly shorter than those of adult males ($F_{1,19} = 83.54$, $P < 0.001$; Table 1).

All the specimens we analyzed had a vertebral ridge process, which is typical for neotropical rattlesnakes. We found paired inter-nasal scales and paired canthal scales in all specimens, whereas the inter-canthals were absent, which is typical for *C. tzabcan*. All specimens had 10 scales bordering the rattle, except for one individual that had 12 scales. Males were significantly different from females only in VEN ($Z = -4.57$, $P < 0.001$), the latter having more scales, and SBC ($Z = 5.97$, $P < 0.001$) and TLB ($Z = 3.14$, $P = 0.001$), both of which were higher in males. We found no significant differences between sexes in MDR ($Z = 1.06$, $P = 0.200$), MTR ($Z = 1.3$, $P = 0.196$), DBB ($Z = 0.43$, $P = 0.662$), WPS ($Z = 0.54$, $P = 0.581$), LPS ($Z = -1.65$, $P = 0.094$), SLS ($Z = -0.64$, $P = 0.513$) or ILS ($Z = -0.69$, $P = 0.488$; Table 2). Finally, we found no significant differences between sexes in the presence of DFI (males = 26 of 33; females = 13 of 19; Fisher's Exact Test, $P = 0.469$; present in 75% of all specimens), PRT (males = five of 33; females = zero of 19; Fisher's Exact Test, $P = 0.144$; absent in 90.4% of all specimens), and PRE-SLS (males = 31 of 33; females = 19 of 19; Fisher's Exact Test, $P = 0.523$; 96.1% of all specimens).

We found that the color pattern of the 22 live and freshly road-killed newborn/ juveniles and adults differed: the newborn/ juveniles were darker than adults, and the largest juvenile with a dark coloration had an SVL of 676 mm, whereas the largest juvenile with a light pattern had an SVL of 680 mm (Table

230

FIGURE 1. A newborn Tzabcan Rattlesnake (*Crotalus tzabcan*) that we found during crepuscular activity at Chichén Itzá, Yucatán, Mexico, 13 July 2015. (Photographed by Rubén Alonso Carbajal-Márquez).

TABLE 2. Morphological character counts of both sexes of the Tzabcan Rattlesnake (*Crotalus tzabcan*; n = 52) captured in the Yucatán Peninsula, and specimens from the Herpetological Collection of El Colegio de la Frontera Sur (ECO-CH-H). Abbreviations are: DBB = dorsal body blotches, ILS = infralabial scales, LPS = number of scales lengthwise on the paravertebral stripes , MDR = midbody dorsal scale rows, MTR = midtail dorsal scale rows, SBC = subcaudal scales, SD = standard deviation, SLS = supralabial scales, TLB = bands on tail, VEN = ventral scales, WPS = number of scales widthwise on paravertebral stripes.

	Male		Female	
	Mean ± SD	range	Mean ± SD	range
VEN	181.3 ± 2.6	175–187	186.6 ± 3.6	181–194
SBC	31 ± 1.0	28–32	23.5 ± 1.1	21–25
MDR	28 ± 1.0	26–29	27.2 ± 0.86	26–29
MTR	12.2 ± 1.2	11–14	11.7 ± 0.64	11–13
DBB	25.1 ± 2.0	20–29	24.9 ± 1.7	21–27
TLB	5.2 ± 3.1	0–9	3.3 ± 2.3	0–6
WPS	2.1 ± 0.41	2–3	2 ± 0.42	1–3
LPS	22.8 ± 6.0	11–38	25.7 ± 5.9	15–42
SLS	15.2 ± 1.2	13–17	15.4 ± 0.98	14–17
ILS	16.1 ± 1.2	14–20	16.2 ± 1.0	14–18

3). Also, coloration between sexes did not differ. All adults were lighter than newborn/ juveniles. Juveniles possess a darker background color and black to brown dorsal blotches (Fig. 1). As they grow, this coloration becomes lighter, and adults display a lighter base color and reddish dorsal blotches (Figs. 3–5).

Crotalus tzabcan activity peaked during the summer (31 records including adults, juveniles, and newborns) and autumn (14 records including juveniles and adults; Fig. 2). Both sexes were equally active in the summer (Nmales = 18, Nfemales = 13) and autumn (Nmales = 10, Nfemales = four; Fisher's Exact Test, *P* = 0.302); however, we only found newborns in the summer. The activity of adults and juveniles did not differ between the summer (Nadults = nine, Njuveniles = seven) and autumn (Nadults = eight, Njuveniles = six; Fisher's Exact Test, *P* = 0.621). There was also no difference in activity between sexes during the summer (Nmales = eight, Nfemales = eight); however, females were more active at the end of this season, and males were slightly more active than females in autumn (Nmales = 10, Nfemales = four). We only found four specimens during the winter (two adult males and one juvenile of each sex) and only two adult males in the spring (Fig. 2). Age classes (Fisher's Exact Test, *P* = 0.120) and sexes (Fisher's Exact Test, *P* = 0.462) did not differ significantly between the dry (November-April) and rainy (May-October) seasons (Fig. 2).

Females were less active during the winter and spring, and we only found a single juvenile specimen in the winter. Meanwhile, we found three males in the winter and two in the spring (Fig. 2). We did not detect enlarged follicles or embryos in the analyzed specimens. Based on the behaviors that we observed, females probably become gravid in late winter and early spring. This coincides with an increase in environmental temperature. After a gestation period of approximately 3–4 mo, they probably gave birth in the summer (June-September). We found the first newborns on 25 June, and they were active in the late afternoon and early hours of the night (Fig.1).

On 26 November 1998 at 2020 in Calakmul, Campeche, Mexico, we found a copulating pair of *C. tzabcan*. We found another pair during copulation 29 November 2016 at 1050 in Calakmul (Fig. 3). We did not take any additional data on either of these occasions so as not to interrupt copulation. Most of the specimens were active (mainly crossing roads) late in the afternoon and during the night in the summer and autumn months. These copulation events and the presence of a subadult individual (probably a female, based on the tail length) basking on a dirt road between Calderitas and Luis Echeverría in northern Chetumal, Quintana Roo, Mexico, 26 November 2016 at 1219 (Fig. 4) indicate that *C. tzabcan* may be active during the day when the temperature drops.

DISCUSSION

Our study provides baseline data about the life history and activity patterns of wild *C. tzabcan* specimens and adds to the morphological data available from previous studies (see Klauber 1952; Armstrong and Murphy 1979; Lee 1996; Campbell and Lamar 2004). The low capture rate of the visual and road surveys and the presence of such a small number of specimens (collected since 1992) in the regional museum, indicate that the Tzabcan Rattlesnake is a secretive species that is difficult to find and follow in the field. This is also true for other species of rattlesnakes, although some are usually abundant (see Klauber 1972; Campbell and Lamar 2004).
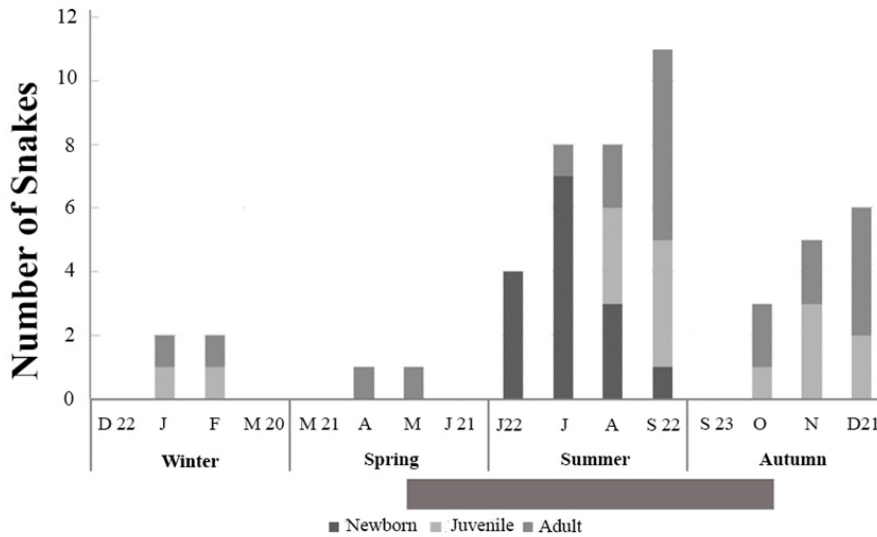
Figure 2. Number of newborns, juveniles, and adults of Tzabcan Rattlesnake (*Crotalus tzabcan*) that we found during this study in the Yucatán Peninsula, per month and season of the year, based on the equinoctial and solstitial periods in the Northern Hemisphere: Spring (21 March to 21 June), Summer (22 June to 22 September), Autumn (23 September to 21 December), and Winter (22 December to 20 March). Gray bar below X axis indicates the rainy season (May-October).

Crotalus tzabcan is sexually dimorphic in TL and HL (females have relatively shorter heads and tails) but not in SVL and TTL. Similarly, the closely related species *C. durissus* and the Central American Rattlesnake (*C. simus*) are also not sexually dimorphic in SVL and TTL, and the sexual difference in TL may be due to the presence of hemipenes (Solórzano and Cerdas 1988; Barros et al. 2012). The degree of sexual dimorphism in *C. tzabcan* SVL is closer to the lower portion of the range reported for other rattlesnakes (-0.01 to -0.29; Shine 1994; Almeida-Santos 2005; Martins et al. 2012).

Additionally, the shorter HL of females suggests that sexual differences may influence the size of prey they consume; however, Carbajal-Márquez et al. (2020a) could not find evidence to support this. Male body size is positively correlated with mating success in many snake species known to have male combat, including rattlesnakes (see Shine 1978). Therefore, this difference in head length between sexes probably favors the combat between males for access to mates, but we are unaware of any published studies that address this relationship. Sexual size dimorphism in head length may also be due

Figure 3. A pair of Tzabcan Rattlesnake (*Crotalus tzabcan*) during copulation in Calakmul, Campeche, Mexico, 29 November 2016. (Photographed by Eduardo M. Pérez-Gámez).

Figure 4. A subadult Tzabcan Rattlesnake (*Crotalus tzabcan*) basking on a dirt road in Chetumal, Quintana Roo, Mexico, 26 November 2016. (Photographed by Fernando A. Aguilar-Santana).

Figure 5. An adult male Tzabcan Rattlesnake (*Crotalus tzabcan*) with a light color pattern found in Yucatán, Mexico. (Photographed by Luis F. Díaz Gamboa).

to phenotypic plasticity in response to environmental factors (Meik et al. 2012), but this requires further testing in future studies.

We found that *Crotalus tzabcan* newborns from different litters were similar in size to those from a clutch of a female captured in the Yucatán (mean TTL of 316 mm, range 290–350 mm, n = 21; Armstrong and Murphy 1979) and what Klauber (1952) observed (mean TTL of 315 mm). The size of newborns, however, varies depending on litter and female body size (Barros et al. 2012; Citadini et al. 2012). Klauber (1952) previously observed sexual dimorphism in VEN (higher number in females) and SBC (higher number in males) in *C. tzabcan* as we recorded in this study. This is also present in other closely related species like the Northwestern Neotropical Rattlesnake (*C. culminatus*), *C. durissus*, Tehuantepec Isthmus Rattlesnake (*C. ehecatl*), Veracruz Neotropical Rattlesnake (*C. mictlantecuhtli*), *C. simus*, and in most species of the genus (Campbell and Lamar 2004; Carbajal-Márquez et al. 2020b). The absence of sexual dimorphism in the other variables reflects the fact that both sexes have similar SVL. The characters related to pholidosis (arrangement of scales) were similar to those Klauber (1952) provided, where all specimens had two internasals, two canthals and no intercanthals. Conversely, we obtained a lower DFI percentage (75% versus 86%); although this was still high enough to segregate them from other closely related species (*C. culminatus* 56%; *C. durissus* 50%; *C. ehecatl* 18.7%; *C. mictlantecuhtli* 0%; *C. simus* 0%; Carbajal-Márquez et al. 2020b).

We observed an ontogenetic color change in *C. tzabcan* from the three Mexican states in the Yucatán Peninsula. All the newborns and juveniles (except the largest juvenile) presented a dark pattern composed of a sulphur yellow-smoke grey background with contrasting black to sepia stripes and blotches and dark spots in the

Table 3. Life stage, sex, and color pattern of the 22 specimens of the Tzabcan Rattlesnake (*Crotalus tzabcan*) we found during this study in the Yucatán Peninsula. Abbreviations are SVL = snout-vent length, TL = tail length, TTL = total length (in mm).

Life Stage	Sex	Color Pattern	SVL	TL	TTL
Newborn	Male	Dark	287	28	315
Newborn	Female	Dark	315	24	339
Newborn	Female	Dark	330	24	354
Newborn	Male	Dark	345	38	383
Newborn	Female	Dark	360	31	391
Newborn	Male	Dark	388	38	426
Juvenile	Female	Dark	415	37	452
Juvenile	Male	Dark	426	41	467
Juvenile	Female	Dark	550	43	593
Juvenile	Male	Dark	655	66	721
Juvenile	Male	Dark	670	66	736
Juvenile	Male	Dark	676	65	741
Juvenile	Female	Light	680	55	735
Adult	Male	Light	743	75	818
Adult	Male	Light	833	75	908
Adult	Male	Light	900	85	985
Adult	Female	Light	1100	90	1190
Adult	Male	Light	1330	142	1472
Adult	Female	Light	1333	95	1428
Adult	Female	Light	1404	100	1504
Adult	Female	Light	1450	100	1550
Adult	Male	Light	1541	168	1709

interspaces. These colors become lighter as they grow and mature. In adults, the background color tends to be light cream, grey or lavender, while the stripes and blotches tend to range from mars brown to mahogany red, and the interspaces have fewer contrasting spots (Fig. 5). Similar to what we observed, Klauber (1952) mentioned that *C. tzabcan* is a snake with conspicuous dark brown, almost black blotches, which sharply contrast with the light gray and brown background, except in very large adults. Klauber (1952) also noted that *C. simus* adults have a less accentuated pattern in comparison with juveniles, although it is important to note that he analyzed preserved specimens with faded coloration. We also noted this trend of lighter adults in wild *C. culminatus* and *C. simus*, which suggests that this may be a shared character in the *C. durissus* species complex.

The overall ground color of rattlesnakes is often closely associated with their habitats (Campbell and Lamar 2004). Therefore, this ontogenetic color change may not only be an indication of sexual maturity but may also be due to the different habitats each life stage uses to bask, forage, or avoid predators (Booth 1990; Farallo and Forstner 2012). Because an ontogenetic change does not exist in the type of prey that *C. tzabcan* consumes (Carbajal-Márquez et al. 2020a), the ontogenetic color change does not appear to be related with the ambush of certain types of prey. Therefore, additional research is needed to elucidate the function of the ontogenetic color change and how it influences *C. tzabcan* behavior.

Crotalus tzabcan possesses a unimodal activity pattern, with peak activity in the summer and autumn. This peak coincides with the rainy season and increased prey availability (Sánchez-Cordero 1993; Adler 1998), so this greater activity may be due to foraging and mating activity. This unimodal pattern is present in the closely related species *C. durissus* (Salomão et al. 1995; Tozetti and Martins 2013). We also only found newborns in this season. Adult males were more active in the autumn when they were most likely searching for females. Females become less active and move less during the winter and spring (dry/cold), probably because they are gravid, while males remain active but to a lesser extent. This coincides with the activity of *C. durissus*, because both sexes show a high site fidelity in the dry/cold season (Tozetti et al. 2009; Tozetti and Martins 2013).

Our results indicate that the daily activity of *C. tzabcan* during the warmer months of the rainy season tend to be crepuscular or nocturnal, and *C. tzabcan* remains active during the cooler months (autumn-winter), especially during the day and during the night if environmental conditions allow it; these observations corroborate those of Lee (1996). This activity pattern is consistent with the relatively high temperatures that are present throughout the year in the Yucatán Peninsula (26–28° C), although temperatures decrease somewhat during the winter (< 22° C; Censky and McCoy 1988; Vidal-Zepeda 2005). Other species from Mexico and the USA such as the Western Diamondback Rattlesnake (*C. atrox*), Sidewinder Rattlesnake (*C. cerastes*), Black-Tailed Rattlesnake (*C. molossus*), and Tiger Rattlesnake (*C. tigris*) also behave in a similar manner (Secor 1994; Beck 1995). Conversely, populations of species from farther north (e.g., Western Rattlesnake [*C. oreganus*] and Prairie Rattlesnake [*C. viridis*]) aggregate in huge numbers in dens during the autumn and winter and cease all activity during this period (Campbell and Lamar 2004).

Because we witnessed *C. tzabcan* mating at the end of November and a decrease in female activity during the winter and spring, it appears that ovulation and fertilization are not synchronous to mating, and females store sperm. Also, we found live specimens with only the pre-button in the summer (from late June to early September); therefore, *C. tzabcan* probably gives birth during this season, similar to anecdotal observations in Quintana Roo and Yucatán (see Dundee et al. 1986; Lee 1996). This pattern coincides with the closely related *C. durissus* and other tropical pitvipers (Saint-Girons 1982; Schuett 1992; Almeida-Santos and Salomão 1997, 2002; Salomão and Almeida-Santos 2002; Almeida-Santos et al. 2004a,b); however, information on the reproductive cycles of closely related species is scarce (see March 1928; Armstrong and Murphy 1979; Solórzano and Cerdas 1988; Solórzano 2004).

Temperate pitvipers also exhibit a similar timing of the female reproductive cycle (Klauber 1972; Schuett 1992), which suggests that this trait is phylogenetically conserved (Almeida-Santos and Salomão 1997; Ji and Wang 2005; Santos et al. 2005; Brown and Shine 2006; Pizzatto et al. 2008). The Pigmy Rattlesnake (*Sistrurus miliarius*), a subtropical pitviper, has a seasonal reproductive pattern that is very similar to other North American pitvipers, except it has an extended mating period (Lind et al. 2018). Therefore, it is possible that the reproductive patterns of subtropical and tropical pitvipers, including *C. tzabcan*, do not exactly match those of their relatives from temperate zones. Therefore, the reproductive cycles of *C. tzabcan* and other neotropical rattlesnake species and pitvipers in general still deserve attention.

Crotalus tzabcan is a large and heavy-bodied snake that reaches an SVL of 1,667 mm and a total length of 1,818 mm (this study), presents sexual dimorphism in tail and head length (longer in males), number of ventral scales (higher in females), subcaudals, and tail bands (higher in males). We observed an ontogenetic color change where newborns and juveniles have a dark background and blotches that become lighter as they mature. *Crotalus tzabcan* possesses a unimodal

activity pattern, with increased activity in the summer and, to a lesser extent, autumn. Depending on weather conditions, it is crepuscular and nocturnal during the warmer months and active during the day in cooler months, which is similar to related species. Our records and behavioral evidence suggest that *C. tzabcan* females possess a reproductive cycle similar to other *Crotalus* species, but additional research is needed. Although current evidence suggests that *C. tzabcan* seems to possess a unimodal mating pattern, the male reproductive cycle needs to be investigated in greater detail. The Tzabcan Rattlesnake is a highly secretive species, difficult to observe and follow in the field. Thus, any information that is accumulated is valuable to obtain a better understanding of its biology and ecology. The life-history data provided herein may be used to optimize how time and funds are spent in monitoring programs. Additional research is needed concerning *C. tzabcan* behavior (activity, movements, habitat use, mating, male to male combat), physiology, histology, and how environmental conditions influence life-history traits to gain a more accurate understanding of the reproductive cycle in both sexes, which could inform conservation strategies.

Literature Cited

Acevedo, M., J. Johnson, and D. Ariano-Sánchez. 2014. *Crotalus tzabcan*. The International Union for Conservation of Nature Red List of Threatened Species 2014. http://www.iucnredlist.org.

Adler, G.H. 1998. Impacts of resource abundance on populations of tropical forest rodent. Ecology 79:242–254.

Almeida-Santos, S.M. 2005. Modelos reprodutivos em serpentes: estocagem de esperma e placentação em *Crotalus durissus* e *Bothrops jararaca* (Serpentes: Viperidae). Ph.D. Thesis, Faculdade de Medicina Veterinária e Zootecnia, Universidade de São Paulo, Brazil. 204 p.

Almeida-Santos, S.M., and M.G. Salomão. 1997. Long-term sperm storage in the Neotropical Rattlesnake *Crotalus durissus terrificus* (Viperidae: Crotalinae). Japanese Journal of Herpetology 17:46–52.

Almeida-Santos, S.M., and M.G. Salomão. 2002. Reproduction in neotropical pitvipers, with emphasis on species of the genus *Bothrops*. Pp. 445–462 *In* Biology of the Vipers. Höggren, M., G.W. Schuett, H. Greene, and M.E. Douglas (Eds.). Eagle Mountain Publishing, Eagle Mountain, Utah, USA.

Almeida-Santos, S.M., F.M.F. Abdalla, P.F. Silveira, N. Yamanouye, M.C. Breno, and M.G. Salomão. 2004a. Reproductive cycle of the neotropical *Crotalus durissus terrificus*: I. Seasonal levels and interplay between steroid hormones and vasotocinase. General and Comparative Endocrinology 139:143–150.

Almeida-Santos, S.M., I.L. Laporta-Ferreira, M.M. Antoniazzi, and C. Jared. 2004b. Sperm-storage in males of the snake *Crotalus durissus terrificus* (Crotalinae: Viperidae) in southeastern Brazil. Comparative Biochemistry and Physiology 139:169–174.

Armstrong, B.L., and J.B. Murphy. 1979. The natural history of Mexican rattlesnakes. University of Kansas Museum of Natural History Publications 5:1–88.

Barros, V.A., L.R. Sueiro, and S.M. Almeida-Santos. 2012. Reproductive biology of the Neotropical Rattlesnake *Crotalus durissus* from northeastern Brazil: a test of phylogenetic conservatism of reproductive patterns. Herpetological Journal 22:97–104.

Beck D. 1995. Ecology and the energetics of three sympatric rattlesnake species in the Sonoran Desert. Journal of Herpetology 29:211–223.

Booth, C.L. 1990. Evolutionary significance of ontogenetic colour change in animals. Biological Journal of the Linnean Society 40:125–163.

Brown, G.P., and R. Shine. 2006. Why do most tropical animals reproduce seasonally? Testing hypotheses on an Australian snake. Ecology 87:133–143.

Campbell, J.A., and W.W. Lamar. 2004. The Venomous Reptiles of the Western Hemisphere. Volume II. USA. Cornell University Press, New York, New York, USA.

Carbajal-Márquez, R.A., J.R. Cedeño-Vázquez, D.

González-Solís, and M. Martins. 2020a. Diet and feeding ecology of *Crotalus tzabcan* (Serpentes: Viperidae). South American Journal of Herpetology 15:9–19.

Carbajal-Márquez, R.A., J.R. Cedeño-Vázquez, A. Martínez-Arce, E. Neri-Castro, and S. Machkour-M´Rabet. 2020b. Accessing cryptic diversity in neotropical rattlesnakes (Serpentes: Viperidae: *Crotalus*) with the description of two new species. Zootaxa 4729:451–481.

Censky, E.J., and C.J. McCoy. 1988. Female reproductive cycles of five species of snakes (Reptilia: Colubridae) from the Yucatán Peninsula, Mexico. Biotropica 20:326–333.

Citadini, J.M., V.A. Barros, G. Puorto, and S.M. Almedia-Santos 2012. Natural history notes: *Crotalus durissus* (Neotropical Rattlesnake). Reproduction. Herpetological Bulletin 119:34–35.

Dundee, H.A., D.A. White, and V. Rico-Gray. 1986. Observations on the distribution and biology of some Yucatan amphibians and reptiles. Bulletin of Maryland Herpetological Society 22:37–50.

Farallo, V.R, and M.R.J. Forstner. 2012. Predation and the maintenance of color polymorphism in a habitat specialist squamate. PLoS ONE 7:1–12. https://doi.org/ 10.1371/journal.pone.0030316.

Gibbons, J.W., and J.E. Lovich. 1990. Sexual dimorphism in turtles with emphasis on the Slider Turtle (*Trachemys scripta*). Herpetological Monographs 4:1–29.

International Union for Conservation of Nature (IUCN). 2001. IUCN Red List categories and criteria: Version 3.1. IUCN Species Survival Commission, Gland, Switzerland.

Ji, X., and Z. Wang. 2005. Geographic variation in reproductive traits and trade-offs between size and number of eggs of the Chinese Cobra (*Naja atra*). Biological Journal of the Linnean Society 85:27–40.

Klauber, L.M. 1940. A statistical study of the rattlesnakes. VII. The rattle. Part 1. Occasional Paper of the San Diego Society of Natural History 6:1–62.

Klauber, L.M. 1952. Taxonomic studies on rattlesnakes of mainland Mexico. Bulletin of the Zoological Society of San Diego 26:1–143.

Klauber, L.M. 1972. Rattlesnakes: Their Habits, Life Histories and Influence on Mankind. 2nd Edition. University of California Press, Berkeley, California, USA.

Lee, J.C. 1996. The Amphibians and Reptiles of the Yucatan Peninsula. Cornell University Press, Ithaca, New York, USA.

Lind, C.M., I.T. Moore, B.J. Vernasco, and T.M. Farrell. 2018. Seasonal testosterone and corticosterone patterns in relation to body condition and reproduction in a subtropical pitviper, *Sistrurus miliarius*. General and Comparative Endocrinology 267:51–58.

Lindenmayer, D., and M. Burgman. 2005. Practical Conservation Biology. CSIRO Publishing, Melbourne, Victoria, Australia.

March, D.D.H. 1928. Field notes on the Neotropical Rattlesnake (*Crotalus terrificus*). Bulletin of the Antivenin Institute of America 2:55–61.

Maritz B., J. Penner, M. Martins, J. Crnobrja-Isailović, S. Spear, L.R.V. Alencar, J. Sigala-Rodríguez, K. Messenger, R.W. Clark, P. Soorae, et al. 2016. Identifying global priorities for the conservation of vipers. Biological Conservation 204:94–102.

Martins, M., G. Arnaud, and H. Ávila-Villegas. 2012. Juvenile recruitment, early growth, and morphological variation in the endangered Santa Catalina Island Rattlesnake, *Crotalus catalinensis*. Herpetological Conservation and Biology 7:376–382.

Meik, J.M, K. Setser, E. Mociño-Deloya and A.M. Lawing. 2012. Sexual differences in head form and diet in a population of Mexican Lance-headed Rattlesnakes, *Crotalus polystictus*. Biological Journal of the Linnean Society 106:633–640.

Pizzatto, L., R.S. Jordão and O.A.V. Marques. 2008. Overview of reproductive strategies in Xenodontini (Serpentes: Colubridae: Xenodontinae) with new data for *Xenodon neuwiedii* and *Waglerophis merremii*. Journal of Herpetology 42:153–162.

Saint-Girons, H. 1982. Reproductive cycles of male snakes and their relationships with climate and female reproductive cycles. Herpetologica 38:5–16.

Salomão, M.G., and S.M. Almeida-Santos. 2002. The reproductive cycle in male Neotropical Rattlesnake (*Crotalus durissus terrificus*). Pp. 507–514 *In* Biology of the Vipers. Schuett, G.W., M. Hoggren, M.E. Douglas, and H.W. Greene. (Eds.). Eagle Mountain Publishing, Carmel, Indiana, USA.

Salomão, M.G., S.M. Almeida-Santos, and G. Puorto. 1995. Activity pattern of *Crotalus durissus* (Viperidae, Crotalidae): feeding, reproduction and snakebite. Studies on Neotropical Fauna and Environment 30:101–106.

Sánchez-Cordero, V. 1993. Estudio poblacional de la rata espinosa *Heteromys desmarestianus* en una selva húmeda de Veracruz, México. Pp 301–316 *In* Avances en el Estudio de los Mamíferos de México. Medellín, R.A., and G. Ceballos (Eds.). Asociación Mexicana de Mastozoología, Asociación Civil, Distrito Federal, Mexico.

Santos, X., G.A. Llorente, M. Feriche, J.M. Pleguezuelos, F. Casals, and A. Sostoa. 2005. Food availability induces geographic variation in reproductive timing of an aquatic oviparous snake (*Natrix maura*). Amphibia-Reptilia 26:183–191.

Schuett, G.W. 1992. Is long-term sperm storage an

important component of the reproductive biology of temperate pitvipers? Pp. 169–170 *In* Biology of the Pitvipers. Campbell, J.A., and Brodie, E.D., Jr. (Eds.). Selva, Tyler, Texas, USA.

Secor, S.M. 1994. Ecological significance of movements and activity range for the Side Winder, *Crotalus cerastes*. Copeia 1994:631–645.

Secretaria de Medio Ambiente y Recursos Naturales, México (SEMARNAT). 2010. Norma Oficial Mexicana NOM-059-SEMARNAT-2010, Protección ambiental. Especies nativas de México de flora y fauna silvestres. Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio. Lista de especies en riesgo. México City, D.F., Mexico. 78 p.

Shine, R. 1978. Sexual size dimorphism and male combat in snakes. Oecologia 33:269–278.

Shine, R. 1994. Sexual size dimorphism in snakes revisited. Copeia 1994:326–346.

Solórzano, A. 2004. Serpientes de Costa Rica. Universidad de Costa Rica, San José, Costa Rica.

Solórzano, A., and L. Cerdas. 1988. Biología reproductiva de la Cascabel Centroamericana *Crotalus durissus durissus* (Serpentes: Viperidae) en Costa Rica. Revista de Biología Tropical 36:221–226.

Torrescano-Valle, N., and W.J. Folan. 2015. Physical settings, environmental history with an outlook on global change. Pp. 9–31 *In* Biodiversity and Conservation of the Yucatán Peninsula. Islebe, G.A., S. Calmé, J.L. León-Cortes, and B. Schmook (Eds.). Springer International Publishing, Cham, Switzerland.

Tozetti, A.M., and M. Martins. 2013. Daily and seasonal activity patterns of free range South-American rattlesnake (*Crotalus durissus*). Anais da Academia Brasileira de Ciências 85:1047–1052.

Tozetti, A.M., V. Vettorazzo, and M. Martins. 2009. Short-term movements of the South American rattlesnake (*Crotalus durissus*) in southeastern Brazil. Herpetological Journal 19:201–206.

Vidal-Zepeda, R. 2005. Las Regiones Climáticas de México. Instituto de Geografía, Universidad Nacional Autónoma de México, Distrito Federal, Mexico.

Wilson, L.D., V. Mata-Silva, and J.D. Johnson. 2013. A conservation reassessment of the reptiles of Mexico based on the EVS measure. Amphibian & Reptile Conservation 7:1–47.

Rubén Alonso Carbajal-Márquez received his Bachelor's degree in Biology from Universidad Autónoma de Aguascalientes (UAA), Aguascalientes, Mexico, his Master's Degree in Use, Management and Conservation of Natural Resources from Centro de Investigaciones Biológicas del Noroeste (CIBNOR), La Paz, Mexico, and Doctoral Degree in Ecology and Sustainable Development from El Colegio de la Frontera Sur (ECOSUR), Chetumal, Mexico. He is member of Conservación de la Biodiversidad del Centro de México A.C., and of the IUCN/SSC Viper Specialist Group. His research interests include biogeography, natural history, ecology, systematics, and conservation of the herpetofauna of Mexico. (Photographed by Tania Ramírez Valverde).

José Rogelio Cedeño-Vázquez is a Biologist from the Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Mexico. He pursued his Master and Doctoral degrees at El Colegio de la Frontera Sur (ECOSUR), Chetumal, Mexico. From 2008–2012 he was a Professor and Researcher at Instituto Tecnológico de Chetumal, Chetumal, Mexico. Rogelio has been a Researcher in the Department of Systematics and Aquatic Ecology at ECOSUR since 2013. His main research interests include systematics, ecology, conservation, and management of herpetofauna. He is associate editor of *Revista Mexicana de Biodiversidad* and *Acta Zoológica Mexicana (nueva serie)*, and is a member of the National System of Researchers of Mexico. (Photographed by N. Gabriela Blanco-Campos).

Marcio Martins is a Professor of Ecology at the University of São Paulo, Brazil. He has published numerous scientific articles on the natural history, ecology, evolution, and conservation of frogs and snakes. His research focuses on understanding (1) the processes that lead to spatial and temporal patterns of diversity of amphibians and reptiles, (2) the evolution of biological characters in these groups, and (3) the processes that lead to patterns of threat and vulnerability in these animals. (Photographed by Nathany Biela).

Gunther Köhler received a degree in Veterinary Medicine (Staatsexamen) at the University Gießen, Giessen, Germany, and a Doctoral degree at Goethe University Frankfurt am Main, Germany; since that time, he has been the Curator of Herpetology at the Senckenberg Research Institute, Frankfurt am Main, Germany. His research focuses on the neotropical herpetofauna, and for three decades he has done field work in Central and South America, Mexico, in the Antilles, and more recently in Myanmar. To date, Gunther has authored or co-authored 27 books and 232 research papers on amphibians and reptiles. (Photographed by Gunther Köhler).