Abstract: The Tehuantepec Isthmus rattlesnake (Crotalus ehecatl) is a poorly known species endemic to Mexico. We describe its diet, morphological variation, life history traits and activity patterns based on data from field encounters, museum specimens, and published data. Its diet consists almost exclusively of mammals, with no detected ontogenetic shift or sexual differences in prey type, and with feeding happening mainly in the rainy season. As the first detailed study on the feeding ecology of C. ehecatl, it adds six new prey species and suggests a homogeneous diet among age classes and sexes, but not among seasons. Crotalus ehecatl does not present sexual dimorphism in snout-vent length, head length or total length, but males have significantly longer tails than females, possess fewer ventral scales, more subcaudal and anterior intersupraocular scales. Crotalus ehecatl showed a unimodal activity pattern with peak activity in the summer, with crepuscular and nocturnal activity during the warmer months, and diurnal activity during the cooler months. The timing of C. ehecatl reproductive events, is similar to other rattlesnakes from temperate and tropical zones. Additional studies on this and related species would help to understand how the ecology of Neotropical rattlesnakes differs from rattlesnakes of more temperate zones.

Keywords: Crotalinae; neotropical rattlesnake; sexual dimorphism; activity pattern; diet

1. Introduction

The Tehuantepec Isthmus rattlesnake (Crotalus ehecatl Carbajal-Márquez, Cedeño-Vázquez, Martínez-Arce, Neri-Castro & Machkour-M’Rabet, 2020), a large and heavy-bodied snake, is endemic to Mexico and is distributed along the Pacific versant from central-south Oaxaca, southward across the Tehuantepec Isthmus to west of Tonalá, Chiapas, almost reaching the Central Valleys in Oaxaca, and in the Grijalva River basin reaching Comitán, Chiapas, from 0 to 1585 m. This species is known from the states of Oaxaca and Chiapas, and may range to southeastern Veracruz, and eastern Huehuetenango, Guatemala. It inhabits mostly open dry areas with rocky outcrops in tropical deciduous forest and seasonal rainforest. Crotalus ehecatl was recently described and previously was considered to belong in part to C. culminatus and C. simus [1–3], and therefore has not been considered in the Red List of the International Union for the Conservation of Nature (IUCN) or the national list of protected species in Mexico [4]. However, factors like climate change, habitat loss, diseases, or the presence of introduced species can cause this species to become threatened. Previous studies have only addressed morphology and anecdotal information on the natural history of this species [5–8], however, behavioral data from the wild are scarce [9].
Detailed studies of natural history of predators and their food habits enable us to place them in a broader ecological and evolutionary context, and this information can be used to evaluate hypotheses about biological diversification, to predict ecological aspects of closely related taxa, and to guide conservation efforts by improving our understanding of trophic webs in ecological assemblages [10–12]. Obtaining data on morphology, life history traits (e.g., time of juvenile recruitment, size at birth, sexual dimorphism), and activity patterns in poorly known species, is critical in understanding organisms [13] and lead to sound conservation strategies.

In this study we explore the taxonomic composition, and the sexual, ontogenetic and seasonal variation in the diet of *C. ehecatl*, and provide information about morphological variation, life history traits, and activity patterns based on specimens that we obtained in recent field surveys, museum collections, literature, and isolated observations throughout most of the distribution range. Our goal was to provide information about the life history and morphology of *C. ehecatl* which will serve as a baseline for future studies on the ecology and conservation of this and related species.

2. Materials and Methods

Sources of data: We obtained dietary, morphological and activity data from 48 specimens, of which 13 were recently sampled live or dead (killed by local people or road-kills) between 2013 and 2020 and deposited in the herpetological collections of El Colegio de la Frontera Sur (ECO-CH-H), Instituto de Biotecnología, Universidad Nacional Autónoma de México (IBT), Universidad Autónoma de Aguascalientes (UAA-REP), and Facultad de Biología, Universidad Juárez del Estado de Durango (UJED-CHFCB), including a specimen that was observed while consuming a bird, as well as one specimen from a natural history note on a predation event [9]. We obtained the remaining data from Laurence M. Klauber historical research notes stored in the archives at the San Diego Natural History Museum, and from specimens deposited in the herpetological collections at Carnegie Museum of Natural History (CM), Museo de Zoología de la Facultad de Ciencias, UNAM (MZFC), Museum of Comparative Zoology, Harvard University (MCZ), and San Diego Natural History Museum (SDNH), covering most of its distribution range (Figure 1; Appendix A). For recently killed and museum specimens, we made a mid-ventral incision to determine the presence of food remains in the stomach and intestines. We measured total length (TTL; ±1 mm), 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 killed snakes. Snake mass was not included because of the inaccuracy of weight measurements associated with preserved specimens. We determined sex by cloacal probing or by evertting hemipenes. Date, locality, number, and identity of prey items were recorded.

Additionally, we obtained data for 15 morphological characters: number of ventral scales (VEN), subcaudal (SBC), midbody dorsal scale rows (MDR), dorsal body blotches (DBB), number of scales widthwise on paravertebral stripes (transverse count; WPS), number of scales lengthwise on the paravertebral stripes (longitudinal count; LPS), number of supralabial scales (SLS), number of infralabial (ILS), number of anterior intersupraoculars (AIS), and presence vs absence of the following characters: intercanthals (ICS), divided first infralabial scale (DFI), postrostral (PRT), contact between the prenasal and the first supralabial scales (PRE-SLS), contact between paravertebral stripes with supraocular scales (PRV-SPO), and interpreeocular scale (IPO). For bilateral characters, we considered the left side, and the right side when damage to the specimen prevented us from recording the former. For scale counts of the width and length of paravertebral stripes, we considered that of the widest and longest stripe. We considered DFI, PRT, PRE-SLS, and IPO when they were present in at least one side of the specimen. In the results, we present these data as mean ± one standard deviation.
Figure 1. Collecting localities of specimens analyzed for the Tehuantepec Isthmus rattlesnake (Crotalus ehecatl) in southern Mexico. Black circles represent recorded localities, state boundaries are indicated by black lines, and the blue area represents the approximate distribution. The insert shows the position of the map in relation to Mexico.

Identification of prey items: Prey remains found in the digestive tract were stored individually in 70% ethanol. To identify mammal prey to genus or species level, dorsal guard hairs were mounted on glass slides and allowed to set for at least 12 h using a glass coverslip [14]. These were then compared with hairs of small mammals (shrews, rodents, lagomorphs, skunks, and marsupials) obtained from the mammalogy collection of ECOSUR (ECO-SC-M) and UAA (UAA-MA), and with keys to the dorsal guard hairs [15,16]. When present, bones, molars, nails, hind limbs, and tails were recovered and used in multiple diagnostics [17]. Additionally, we used the known geographic distribution of prey species as a criterion to reach species-level identification.

Analyses: We tested for differences in SVL and TTL between adults and all specimens (newborns, juveniles and adults) of both sexes with the independent-samples t-test, after we log transformed all variables to meet assumptions of parametric testing. We calculated the degree of sexual size dimorphism in SVL following Gibbons and Lovich [18] and Shine [19]. We used Analyses of Covariance (with SVL as the covariate) to detect differences in TL and HL between ages and sexes, after we log transformed all variables, and we tested the assumption of homogeneity of regression slopes by the interaction of sex and snake length. We performed non-parametric Fisher’s Exact Test to compare proportions of specimens containing food items between juveniles and adults, males and females, and seasons; the same test was used to compare consumed prey types between sexes, and age classes.

We performed Mann-Whitney U-tests for ordinal scale characters, and Fisher’s Exact Test for nominal scale characters to compare males and females. For all these analyses, we
considered an individual to be a newborn when it only had a prebutton (or birth-rattle), a single button (first permanent rattle) or a button with a second rattle [20]; a juvenile when it had a TTL < 800 mm and with more than two rattle segments on the rattle; and an adult if it had a TTL ≥ 800 mm (based on the minimum reproductive size of the closely related South American Rattlesnake, *C. durissus* [21–23]). 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). To assess temporal variation in the diet and activity, we considered the month of collection as well as the season based on precipitation: rainy (May–October, >60 mm per month) or dry (November–April, <60 mm per month) season [24]. We used Fisher’s Exact Test to evaluate capture frequency differences in age classes, sexes, and specimens with food content among seasons. We performed all statistical analyses in Statistica [25] (StatSoft Inc., Tulsa, Oklahoma, USA), and considered results to be statistically significant when \( p \leq 0.05 \).

3. Results

3.1. Prey Items

Of the 48 *C. ehecatl* specimens examined, 17 (35.4%) contained a total of 18 prey items, 15 in the hindgut, one specimen found consuming a Northern Bobwhite (*Colinus virginianus*), and another consuming a West Mexican Cotton Rat (*Sigmodon mascotensis*). Only one snake contained multiple prey items (remains of an unidentified bird and a mammal). Eleven fecal contents (61.1%) were identified to class level as unidentified mammal (10) and unidentified bird (one). We identified 16 mammalian prey items (88.9% of diet) consisting of six species representing three orders and two avian prey items (11.1%) including one identified species (Table 1).

Table 1. Frequency and percentage of occurrence of the taxa that comprise the diet of Tehuantepec Isthmus rattlesnake (*Crotalus ehecatl*) from specimens analyzed in this study, from Klauber [6], and Carbajal-Márquez et al. [9].

<table>
<thead>
<tr>
<th>Prey Taxon</th>
<th>Frequency</th>
<th>%</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mammalia</td>
<td>16</td>
<td>88.9</td>
<td>Klauber 1972, This study</td>
</tr>
<tr>
<td>Unidentified mammal</td>
<td>10</td>
<td>56</td>
<td></td>
</tr>
<tr>
<td>Soricomorpha</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soricidae</td>
<td>1</td>
<td>5.5</td>
<td>This study</td>
</tr>
<tr>
<td>Lagomorpha</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sylvilagus brasiliensis</em></td>
<td>1</td>
<td>5.5</td>
<td>This study</td>
</tr>
<tr>
<td>Rodentia</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cricetidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Baiomys musculus</em></td>
<td>1</td>
<td>5.5</td>
<td>This study</td>
</tr>
<tr>
<td><em>Peromyscus sp.</em></td>
<td>1</td>
<td>5.5</td>
<td>This study</td>
</tr>
<tr>
<td><em>Sigmodon hispidus</em></td>
<td>1</td>
<td>5.5</td>
<td>This study</td>
</tr>
<tr>
<td><em>Sigmodon mascotensis</em></td>
<td>1</td>
<td>5.5</td>
<td>Carbajal-Márquez et al., 2021</td>
</tr>
<tr>
<td>Aves</td>
<td>2</td>
<td>11.1</td>
<td></td>
</tr>
<tr>
<td>Unidentified bird</td>
<td>1</td>
<td>5.5</td>
<td>Klauber 1972</td>
</tr>
<tr>
<td>Odontophoridae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Colinus virginianus</em></td>
<td>1</td>
<td>5.5</td>
<td>This study</td>
</tr>
<tr>
<td>Total</td>
<td>18</td>
<td>100</td>
<td></td>
</tr>
</tbody>
</table>

Dietary items were obtained from two newborns (355–400 mm), six juveniles (440–685 mm) and nine adults (751–1519 mm). The probability of containing food items was similar in newborn plus juveniles (34.8% of 23 specimens) and adult snakes (36% of 25; Fisher’s Exact Test, \( p = 0.58 \)). Prey class (Mammalia and Aves) was independent of snake SVL (\( Z = 1.41, p = 0.15; \) Figure 2) and age class, with similar proportions of mammals consumed by newborn plus juvenile (100%, \( n = 8 \)) and adult snakes (88.8%, \( n = 9 \); Fisher’s Exact Test, \( p = 0.29 \)). Males (55.5%, \( n = 18 \)) and females (22.2%, \( n = 27 \)) were not equally likely to
contain prey items (Fisher’s Exact Test, \( p = 0.02 \)). There was no significant difference in prey class (Mammalia and Aves) consumed between sexes (Fisher’s Exact Test, \( p = 0.59 \)). From 43 specimens with collection dates, we recovered 15 prey items from June to November (Figure 3), and three without date. The presence of prey was concentrated in the rainy season with 14 specimens with prey (all mammals), and one specimen (avian) in the dry season. No significant difference was found in the proportion of specimens with prey items (Fisher’s Exact Test, \( p = 0.64 \)) between rainy and dry seasons. Also, no significant difference was found in males and females with prey items between rainy/dry seasons (Fisher’s Exact Test, \( p = 0.35 \); excluding one specimen without collection date, and one with unknown sex).

![Figure 2. Relationship between prey types (Aves and six different mammal categories) and snake snout-vent length (SVL, in mm) of individuals of Tehuantepec Isthmus rattlesnake (Crotalus ehecatl).](image)

### 3.2. Snake Size Distribution

Snout-vent length ranged between 343 and 1519 mm (776.7 ± 319.2; \( n = 42 \)) and TTL between 371 and 1656 mm (846.10 ± 348.23 mm; \( n = 42 \)). The largest male in our sample measured 1532 mm TTL (SVL = 1381 mm, TL = 151 mm), and the largest female, 1656 mm TTL (SVL = 1519 mm, TL = 137 mm). Among adults, mean female SVL was 1067.5 ± 225.2 mm (\( n = 13 \)) and 5.0% larger than that of males (1016.4 ± 258.2 mm SVL; \( n = 7 \)), with no significant difference (\( t = −0.51 \), \( df = 18 \), \( p = 0.61 \)). The degree of sexual size dimorphism in SVL was 0.08. The SVL between male (740.4 ± 308.8; \( n = 16 \)) and females (799 ± 329.5; \( n = 26 \)) of all specimens (newborn, juveniles and adults) did not vary significantly (\( t = −0.48 \), \( df = 40 \), \( p = 0.63 \)). We found no significant difference in TTL between sexes of adults (\( t = −0.22 \), \( df = 18 \), \( p = 0.82 \)), and all specimens (\( t = −0.41 \), \( df = 40 \), \( p = 0.68 \)), but adult females were generally longer. The TL of adult males (115 ± 31.7 mm; \( n = 7 \)) was significantly longer (\( F_{1,17} = 49.85 \), \( p < 0.001 \)) than that of adult females (84.2 ± 19.7 mm; \( n = 13 \)); the effect of snake length in this ANCOVA model was also significant (\( F_{1,17} = 76.77 \), \( p < 0.001 \)), and the interaction between the snake length and sex was not significant (\( F_{1,17} = 0.05 \), \( p = 0.82 \)). We also found a significant difference in TL for all male (\( n = 16 \)) and female (\( n = 26 \)) specimens (\( F_{1,30} = 46.27 \), \( p < 0.001 \)); the effect of snake length was also significant (\( F_{1,17} = 354.37 \), \( p < 0.001 \)), and the interaction between the snake length and
sex was not significant ($F_{1,17} = 0.01, p = 0.91$). We found no significant difference in HL ($F_{1,13} = 1.77, p = 0.20$) between adult females ($n = 11$) and adult males ($n = 5$); the effect of snake length in this model was significant ($F_{1,13} = 6.54, p = 0.02$), but the interaction between the snake length and sex was not significant ($F_{1,13} = 0.01, p = 0.89$). For all male ($n = 13$) and female ($n = 21$) specimens we found no significant difference in HL ($F_{1,31} = 0.77, p = 0.38$; Table 2); with a significant effect of snake length ($F_{1,31} = 126.43, p < 0.001$), and the interaction between the snake length and sex was not significant ($F_{1,31} = 1.05, p = 0.31$).

![Figure 3](image-url) Monthly percentages of prey items of Tehuantepec Isthmus rattlesnake (Crotalus ehecatl). Numbers in parentheses are specimens found per month. Note the high number of specimens found in the rainy season (May–October).

**Table 2.** Sample sizes ($n$), mean ($±$ standard deviation), and range (below means) of snout-vent length (SVL, mm), tail length (TL, mm), total length (TTL, mm), and head length (HL, mm) of newborn, juvenile, and adult Tehuantepec Isthmus rattlesnake (Crotalus ehecatl) specimens. Abbreviations are: NM = newborn male, NF = newborn female, JM = juvenile male, JF = juvenile female, AM = adult male, AF = adult female.

<table>
<thead>
<tr>
<th></th>
<th>NM</th>
<th>NF</th>
<th>JM</th>
<th>JF</th>
<th>AM</th>
<th>AF</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>n</strong></td>
<td>1</td>
<td>6</td>
<td>8</td>
<td>7</td>
<td>7</td>
<td>13</td>
</tr>
<tr>
<td><strong>SVL</strong></td>
<td>355</td>
<td>414 ± 75.2</td>
<td>547.1 ± 84.1</td>
<td>630.1 ± 92.0</td>
<td>1016.4 ± 258.2</td>
<td>1067.5 ± 225.2</td>
</tr>
<tr>
<td><strong>TL</strong></td>
<td>35</td>
<td>35.5 ± 10.2</td>
<td>54.4 ± 10.2</td>
<td>48.0 ± 8.1</td>
<td>115.0 ± 31.7</td>
<td>84.2 ± 19.7</td>
</tr>
<tr>
<td></td>
<td>28–49</td>
<td>45–75</td>
<td>38–57</td>
<td>81–155</td>
<td>62–137</td>
<td></td>
</tr>
<tr>
<td><strong>TTL</strong></td>
<td>390</td>
<td>449.5 ± 85.0</td>
<td>601.5 ± 93.4</td>
<td>737.7 ± 123.6</td>
<td>1131.0 ± 287.5</td>
<td>1151.8 ± 243.0</td>
</tr>
<tr>
<td><strong>n</strong></td>
<td>1</td>
<td>5</td>
<td>7</td>
<td>5</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td><strong>HL</strong></td>
<td>20</td>
<td>25.2 ± 3.1</td>
<td>32.0 ± 3.6</td>
<td>33.6 ± 2.6</td>
<td>43.2 ± 10.8</td>
<td>46.8 ± 7.1</td>
</tr>
<tr>
<td></td>
<td>20.8–28.3</td>
<td>27.6–36.0</td>
<td>30.6–36.3</td>
<td>27.8–54.4</td>
<td>35.9–55.8</td>
<td></td>
</tr>
</tbody>
</table>
3.3. Sex Differences

Males were significantly different from females only in AIS, and SBC both of which were higher in males, and VEN with more scales in females. We found no significant differences between sexes in DBB, ILS, LPS, MDR, SLS, or WPS (Table 3). We found paired inter-nasal scales and paired canthal scales in all specimens, whereas the presence or absence of ICS did not vary significantly between males and females. Finally, we found no significant differences between sexes in the presence of DFI (present in 23.9% of all specimens, \( n = 46 \); two with sex undetermined), IPO (42.1% of all specimens, \( n = 19 \); one with sex undetermined), PRE-SLS (95.6% of all specimens, \( n = 46 \); two with sex undetermined), and PRV-SPO (71.4% of all specimens, \( n = 21 \); one with sex undetermined; Table 3).

Table 3. Morphological character counts of male and female Tehuantepec Isthmus rattlesnake (Crotalus ehecatl; \( n = 47 \)). Abbreviations are: AIS = anterior intersupraoculars, DBB = dorsal body blotches, DFI = divided first infralabial scale, ICS = intercanthal scales, ILS = infralabial scales, IPO = interpreocular scale, LPS = number of scales lengthwise on the paravertebral stripes, MDR = midbody dorsal scale rows, PRE-SLS = contact between the prenasal and the first supralabial scales, PRT = postrostral scale, PRV-SPO = contact between paravertebral stripes with supraocular scales, SBC = subcaudal scales, SD = standard deviation, SLS = supralabial scales, VEN = ventral scales, WPS = number of scales widthwise on paravertebral stripes.

<table>
<thead>
<tr>
<th>Character</th>
<th>Male Mean ± SD</th>
<th>Male Range</th>
<th>Female Mean ± SD</th>
<th>Female Range</th>
<th>Mann-Whitney U-Tests</th>
<th>Fisher’s Exact Test</th>
</tr>
</thead>
<tbody>
<tr>
<td>AIS</td>
<td>3.3 ± 0.6</td>
<td>3–5</td>
<td>2.8 ± 0.9</td>
<td>2–5</td>
<td>Z = 1.99, ( p = 0.04 )</td>
<td>–</td>
</tr>
<tr>
<td>DBB</td>
<td>27.8 ± 2.7</td>
<td>23–31</td>
<td>28.2 ± 1.7</td>
<td>25–32</td>
<td>Z = −0.23, ( p = 0.81 )</td>
<td>–</td>
</tr>
<tr>
<td>ILS</td>
<td>15.7 ± 1.4</td>
<td>13–19</td>
<td>16.1 ± 1.3</td>
<td>13–18</td>
<td>Z = −1.20, ( p = 0.22 )</td>
<td>–</td>
</tr>
<tr>
<td>LPS</td>
<td>20.3 ± 6.7</td>
<td>9–31</td>
<td>25.8 ± 5.1</td>
<td>19–35</td>
<td>Z = −1.88, ( p = 0.05 )</td>
<td>–</td>
</tr>
<tr>
<td>MDR</td>
<td>27.8 ± 1.3</td>
<td>26–31</td>
<td>28.4 ± 1.2</td>
<td>27–31</td>
<td>Z = −1.25, ( p = 0.21 )</td>
<td>–</td>
</tr>
<tr>
<td>SBC</td>
<td>29.2 ± 1.9</td>
<td>26–32</td>
<td>23.1 ± 1.5</td>
<td>21–26</td>
<td>Z = 5.57, ( p &lt; 0.001 )</td>
<td>–</td>
</tr>
<tr>
<td>SLS</td>
<td>14.7 ± 0.9</td>
<td>13–17</td>
<td>14.8 ± 0.8</td>
<td>13–16</td>
<td>Z = −0.34, ( p = 0.72 )</td>
<td>–</td>
</tr>
<tr>
<td>VEN</td>
<td>176.3 ± 5.4</td>
<td>168–186</td>
<td>183.4 ± 3.1</td>
<td>177–187</td>
<td>Z = 4.10, ( p &lt; 0.001 )</td>
<td>–</td>
</tr>
<tr>
<td>WPS</td>
<td>2.1 ± 0.6</td>
<td>1–3</td>
<td>2.3 ± 0.5</td>
<td>2–3</td>
<td>Z = −0.64, ( p = 0.52 )</td>
<td>–</td>
</tr>
<tr>
<td>ICS</td>
<td>4 of 15</td>
<td>2–5</td>
<td>10 of 26</td>
<td>1–5</td>
<td>–</td>
<td>( p = 0.33 )</td>
</tr>
<tr>
<td>DFI</td>
<td>6 of 18</td>
<td>–</td>
<td>5 of 26</td>
<td>–</td>
<td>–</td>
<td>( p = 0.23 )</td>
</tr>
<tr>
<td>IPO</td>
<td>4 of 8</td>
<td>–</td>
<td>4 of 10</td>
<td>–</td>
<td>–</td>
<td>( p = 0.07 )</td>
</tr>
<tr>
<td>PRE-SLS</td>
<td>18 of 18</td>
<td>–</td>
<td>24 of 26</td>
<td>–</td>
<td>–</td>
<td>( p = 0.34 )</td>
</tr>
<tr>
<td>PRT</td>
<td>2 of 18</td>
<td>–</td>
<td>9 of 26</td>
<td>–</td>
<td>–</td>
<td>( p = 0.50 )</td>
</tr>
<tr>
<td>PRV-SPO</td>
<td>7 of 10</td>
<td>–</td>
<td>8 of 10</td>
<td>–</td>
<td>–</td>
<td>( p = 0.52 )</td>
</tr>
</tbody>
</table>

3.4. Seasonal Variation

Crotalus ehecatl activity peaked during the summer (29 records including newborns, juveniles and adults) followed by autumn (seven records including newborns, juveniles and adults; Figure 4). Both sexes were equally active in the summer (Nmales = 12, Nfemales = 16) and autumn (Nmales = one, Nfemales = five; Fisher’s Exact Test, \( p = 0.23 \)). The activity of adults and newborn plus juveniles did not differ between the summer (Nadults = 14, Njuveniles = 15) and autumn (Nadults = three, Njuveniles = four; Fisher’s Exact Test, \( p = 0.56 \)). There was also no difference in activity between adults of both sexes during the summer (Nmales = three, Nfemales = 10) and autumn (Nmales = one, Nfemales = one; Fisher’s Exact Test, \( p = 0.47 \)). We only found two specimens during the winter (one adult female and one juvenile female) and four during spring (two adult males, one adult female, and one adult with sex undetermined; Figure 4). Age classes (Fisher’s Exact Test, \( p = 0.47 \)) and sexes (Fisher’s Exact Test, \( p = 0.08 \)) did not differ significantly between the dry (November-April) and rainy (May-October) seasons (Figure 4). Females were more active during the winter (Nmales = 0, Nfemales = two), equal between sexes in the spring (Nmales = two, Nfemales = two, and one with sex undetermined), and we only
found a single juvenile specimen in the winter and one in the spring. We did not detect enlarged follicles or embryos in the analyzed specimens. We found the first newborns on 26 June, and they were active in the late afternoon and early hours of the night, while adults can also be active in the early morning.

**Figure 4.** Number of newborns, juveniles, and adults of Tehuantepec Isthmus rattlesnake (*Crotalus ehecatl*) analyzed during this study, by 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).

### 4. Discussion

**Diet variation:** Our study provides baseline data about the feeding habits, life history and activity patterns of wild *C. ehecatl* specimens and adds to the morphological data available from previous studies. Previously, only unidentified rodents and one unidentified bird had been mentioned as prey (under the synonym of *C. d. durissus*, see Klauber [6]), and a note reporting *S. mascotensis* [9]. Although Álvarez del Toro [8] mentions that the Neotropical rattlesnakes of Chiapas feeds on rats, gophers, rabbits, and birds, our results revealed that *C. ehecatl* specializes in consuming mammalian prey, and it rarely feeds on birds. Terrestrial rodents were the main prey source, followed by birds. This high intake of mammals coincides with *C. simus* and *C. tzabcan*, which also consume mainly terrestrial rodents [26,27]. Ectothermic prey (e.g., arthropods, amphibians, lizards, snakes) were absent in our samples, suggesting that they are rarely consumed, even when those prey types are abundant in the region where *C. ehecatl* occurs and are consumed by other sympatric pitvipers [2,8]. Therefore, the preference for endotherms, is probably not related to prey availability. Other medium to large sized rattlesnakes also show a specialization in mammalian prey including closely related species like *C. durissus* [28–30], *C. simus* [27], *C. tzabcan* [26], and *C. ornatus* [31], as well as other not so closely related species such as *C. adamantacus* [32], *C. atrox* [33], *C. horridus* [34], and *C. ruber* [35].
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Crotalus ehecatl newborns are relatively large at birth, and we found two individuals (355 and 400 mm SVL) with mammal remains in their guts. We did not find significant differences between the size and age class of the snakes regarding the type of prey consumed, thus, indicating that C. ehecatl feeds on mammals at all stages of life. Juvenile snakes specialized in consuming mammals are likely to grow faster, avoiding prolonged exposure to predators, and attaining sexual maturity more quickly [26]. Additionally, the diet of the closely related species C. basiliscus, C. culminatus, C. durissus, C. molossus, C. ornatus, C. simus, C. totonacus and C. tzabcan [3,6,26,36] is also mostly composed of endotherms, a trait that is probably ancestral in this group [34].

Due to the advanced degree of digestion of the prey recovered from C. ehecatl specimens, we could not obtain prey size. However, we did not expect differences in prey size consumed by males and females, since there is no significant difference in SVL between sexes. Furthermore, this absence of sexual differences in prey size has been confirmed in C. durissus [29], C. tzabcan [26], and other non Neotropical rattlesnakes that do not show difference in prey size consumed between sexes like C. atrix [37], C. catalinensis [38], C. cerastes [39], C. willardi [40], and S. catenatus [41], not even when sexual size dimorphism was evident, as in C. enyo [42]. However, there are also species with sexual size dimorphism that differed in prey consumption like C. lutosus [43]. Vipers are characterized by their large gape and stoutness that facilitate predation on large prey [10,44], and that is probably the reason that an apparent pattern is not perceived in the diet of most rattlesnakes with or without sexual dimorphism.

Crotalus ehecatl feeds mainly in the rainy season in the same way as other rattlesnakes from temperate regions [7,33,43,45,46], which could be tied to reproduction in addition to precipitation. However, they probably continue feeding in the dry season if there are suitable climatic conditions, like C. tzabcan, which can feed throughout the year [26]. This feeding pattern found in C. ehecatl is mainly due to the fact that the rainy season coincides with the warmer months [24], which turns its activity to crepuscular and nocturnal, matching the activity of most rodents, and also with the increase in the availability of prey in the region where this species occurs. Closely related C. culminatus is mainly nocturnal, with a peak of activity in the rainy season, and only mammals have been reported in its diet to date [6,7,47]. Also, C. cerastes increase the rodent consumption during warmer months [39].

Size and morphology variation: Adult males and females of C. ehecatl have a similar body size. These results parallel those of C. durissus and C. tzabcan in which males and females do not exhibit sexual dimorphism in SVL and TTL [23,26,29,48]. Also, in C. simus from Costa Rica, males have only a slightly higher TTL than females [49]. Larger male size in snakes seems to be related to combat between males [50–52]. However, this behavior has been reported for C. durissus and C. simus, and probably occurs in C. tzabcan, none of which show significant differences in body size [26,27,53,54]. Thus, we expect that C. ehecatl will also present male–male combat behavior. Crotalus ehecatl is sexually dimorphic in TL (females have relatively shorter tails). Similarly, the closely related species C. durissus, C. simus and C. tzabcan are also sexually dimorphic in TL, and may be due to the presence of hemipenes [23,26,48,49]. The degree of sexual dimorphism in C. ehecatl SVL is closer to the lower portion of the range reported for other rattlesnakes and similar to C. durissus and C. tzabcan (−0.01 to −0.29; [17,48,55,56]). Additionally, the absence of HL dimorphism in C. ehecatl suggests that there are no differences in the type and size of prey consumed between sexes, which was supported in this study, at least in terms of the type of prey. In contrast, Carbajal-Márquez et al. [26,48] found difference in the HL of adults of C. tzabcan where the females have a shorter head than males, but there was no significant difference in type and prey mass between sexes. Difference in head length between sexes probably favors the combat between males for access to mates [50], therefore, this lack in HL difference between sexes in C. ehecatl could indicate the absence of combat between males, but as mentioned above, male–male combat has been reported in C. durissus and C. simus, even when differences in body size are minimal between sexes.
We found that *C. ehecatl* newborns from different litters were similar in size to those reported for *C. tzabcan* by Klauber [5] (mean TTL of 315 mm), Armstrong & Murphy [7] (mean TTL of 316 mm, range 290–350 mm, *n* = 21), and Carbajal-Márquez et al. [26,48] (male mean TTL of 363.1 mm, range 285–426 mm, *n* = 10, female mean TTL of 360.6 mm, 330–391 mm, *n* = 5), and for *C. simus* (275–430 mm; [27]). However, the size of newborns in *C. durissus* varies depending on litter and female body size [23,57].

We also found significant differences between sexes of *C. ehecatl* in AIS, SBS (higher number in males) and VEN (higher number in females), and no significant difference in the remainder of measured morphological characters. This pattern of morphological variation coincides with that previously observed in Neotropical rattlesnakes like *C. culminatus*, *C. durissus*, *C. mictlantecuhtli*, *C. simus*, *C. tzabcan*, as well as in most of the species of the genus [2,3,5,48]. We further found no significant difference in MDR, DBB, WPS, LPS, SLS, ILS, ICS, DFI, PRT, PRE-SLS, PRV-SPO, and IPO; thus, the absence of sexual dimorphism in these variables reflects the fact that both sexes have similar body size. We obtained a higher percentage of ICS (34.1% vs. 18.7%), DFI (23.9% vs. 18.7%), PRT (23.9% vs. 12.5), PRE-SLS (95.6% vs. 93.7%), PRV-SPO (71.4% vs. 68.7%), and lower IPO percentage (42.1% vs. 50%), than previously reported for *C. ehecatl* [3].

**Activity pattern variation:** *Crotalus ehecatl* possesses a unimodal activity pattern, with an activity peak in the summer and to a lesser extent in autumn. This peak coincides with the rainy season and increased temperature and prey availability [24,58,59]. Armstrong & Murphy [7] mentioned that *C. ehecatl* specimens found in the Tehuantepec Isthmus were active in June, three weeks after the rains started, and specimens were found active at night on the road, and several found in the afternoon when rains were in the form of light drizzle. This unimodal activity pattern is also present in the closely related species *C. culminatus*, *C. durissus*, *C. totonacus*, and *C. tzabcan*, and in many rattlesnakes [2,7,29,48,60]. Adult both sexes were more active in the summer and autumn when they were most likely searching for food and mates. Females become less active and move less during the winter and spring (dry/cold season), probably because they are gravid, but also males reduce their activity. This decrease in activity coincides with *C. durissus* and *C. tzabcan*, which show a high site fidelity during the dry/cold season [48,60,61]. We found most newborns in summer and one at the end of autumn, and most juveniles were found in summer, coinciding with *C. tzabcan* [48]. This activity pattern suggests that in *C. ehecatl*, ovulation and fertilization are not simultaneous to mating, and females store sperm. Probably mating occurs in late fall and winter, they become pregnant in late winter and spring, and hatchlings are born during summer. This coincides with the closely related *C. durissus* [21,22,62–64], *C. simus* [27], *C. tzabcan* [48], and other tropical pitvipers [65,66]. Many pitvipers from more temperate zones also exhibit a similar timing of the female reproductive cycle [6,65,67,68], which suggests that this trait is phylogenetically conserved [62,69,70]. Mating behavior events of snakes documented in the wild are scarce, including Neotropical rattlesnakes, which can be due to their secretive habits and low encounter rate. To date only two copulation events have been documented in the field for *Crotalus tzabcan*, and one for *C. durissus* [48,64]. Thus, the mating behavior and reproductive cycles of *C. ehecatl* and other Neotropical rattlesnake species and pitvipers in general still deserve attention.

Our diet results, where most of the prey were rodents, indicate that the daily activity of *C. ehecatl* during the warmer months of the rainy season tend to be crepuscular or nocturnal, although it can remain active in the early hours of the day (1000 h) as evidenced by a predation event on a *S. mascotensis* [9]. Also, *C. ehecatl* can remain active during the cooler months (autumn-winter), especially during the day and probably during the night if environmental conditions allow it. This daytime activity during the autumn can be supported as an adult female was observed preying on a *C. virginianus* at 1004 h on November 25 of 2016; this coincides with diurnal activity of *C. tzabcan* during the dry/cold months [48].

Our study provides baseline data about the feeding ecology, life history and activity patterns of *C. ehecatl* specimens and adds to the morphological data available from previous
studies [2,5–7]. Additionally, our findings provide a better understanding of the taxonomic composition of the diet of *C. ehecatl* and patterns of dietary variation and generate inferences about the feeding behavior of this rattlesnake. *Crotalus ehecatl* is a specialized mammal predator, and therefore similar to its close relatives *C. culminatus*, *C. durissus*, *C. simus* and *C. tzaban*. Our sample size is relatively small, reflecting the rarity of this species, the difficulty of finding recently fed specimens, and infrequent collection. Although our simple size suggests caution in interpreting our results, the almost exclusive intake of endotherms (mainly mammals and birds to a lesser extent) and rarely ectotherms is a pattern also observed in closely related species. *Crotalus ehecatl* is a large and stout snake that reaches an SVL of 1519 mm and a total length of 1656 mm (this study), presents sexual dimorphism in tail length (longer in males), number of ventral scales (higher in females), subcaudals, and anterior intersupraoculars (higher in males). We observed a unimodal activity pattern, with increased activity in the summer and, to a lesser extent in 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. ehecatl* seems to possess a unimodal mating pattern, however, the reproductive cycle in both sexes needs to be investigated in greater detail. *Crotalus ehecatl*, as other Neotropical rattlesnakes, is a highly secretive species, difficult to study in the field. Therefore, the natural history and morphological data provided herein help to obtain a better understanding of its biology and ecology. Currently, snakes in general face several threats to their survival such as climate change, introduction of invasive species, mortality associated with habitat loss, human encounters, and road traffic, illegal species trafficking, and even capture for scientific purposes [71]. This species is also hunted for the healing properties that the local people attribute to it [72,73]. Further research on the biology, natural history and behavior of *C. ehecatl* and related species would help us better understand how the ecology of Neotropical rattlesnakes compares to those of more temperate regions, and to optimize how time and funds are spent in monitoring programs, and eventually lead to better conservation strategies.


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**Institutional Review Board Statement:** The study was conducted according to the guidelines of the federal regulations in México “Norma Oficial Mexicana NOM-062-ZOO-1999, Especificaciones técnicas para la producción, cuidado y uso de los animales de laboratorio” and “Norma Oficial Mexicana NOM-126-ECOL-2000, Especificaciones para la realización de actividades de colecta científica de material biológico de especies de flora y fauna silvestres y otros recursos biológicos en el territorio nacional”, and approved by the Departamento de Apoyo a la Investigación, Universidad Autónoma de Aguascalientes, Protocol PIB21-4, approved on December 2020.

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**Data Availability Statement:** Data are available from the authors upon request. The data are not publicly available due to the author’s policy of saving unpublished data for future publications.
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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

_Crotalus ehecatl_ (n = 48). MEXICO: CHIAPAS: 12.2 km west of Chiapa de Corzo, municipality of Chiapa de Corzo (ECOH-H 3776); San José Tintonishac, municipality of San José Tintonishac (IBT 084); Las Maravillas, Villa de Corzo (MZFC 23990); Galecio Narcia, municipality of Tonalá (MCZ-R 5036); 8 km southeast of San Vicente La Mesilla, municipality of Tzimol (UAAREP 807); 2.4 km west of El Triunfo, municipality of La Independencia (UAAREP 795); 2 km southeast Las Margaritas, municipality of Las Margaritas, municipality of La Independencia (UAAREP 782, 794, field specimen); Arriaga, municipality of Arriaga (CAS HERP 163538); 10.3 km northwest of Tuxtla Gutiérrez, municipality of San Fernando (UIMNH 6270); Rancho San Bartolo, municipality of Cintalapa (UIMNH 10000, 10001); Comitán, municipality of Comitán de Domínguez (UIMNH 19173). OAXACA: Salina Cruz, municipality of Salina Cruz (UJED-CHFCB 3079); Santo Domingo, Zanatepec, municipality of Santo Domingo Zanatepec (UJED-CHFCB 3079); San Pedro Tapanatepec, municipality of San Pedro Tapanatepec (MCZ-R 27819–27825, SDNHM 24383, UJED-CHFCB 0380); La Ventosa, municipality of Juchitán de Zaragoza (field specimen); Tehuantepec, municipality of Santo Domingo Tehuantepec (AMNH 64601, 65173, MCZ-R 50645, UIMNH 19174, UMMZ Herps 82754–82756, 89990, 89991, UMNH Herp 2743, USNM 30260); 2mi E Puerto Escondido, municipality of Santa María Chimalapa (CM-Herps 69448); 5mi W of Tehuantepec, municipality of Santo Domingo Tehuantepec (CM-Herps 69449), Pluma Hidalgo, municipality of Pluma Hidalgo (AMNH 19855); 3.1 km west of La Soledad, municipality of Santo Domingo Petapa (UIMNH 6269); 14.2 km southeast Santa María Chimalapa, municipality of Santa María Chimalapa (UIMNH 32555); San Pedro Huilitopec, municipality of San Pedro Huilitopec (UMMZ Herps 82753, USNM 46473); 28 km west of Las Vacas, municipality of Magdalena Tequisistlán (USNM 110612); 3.5 km south of Santo Domingo Ingenio, municipality of Santo Domingo Ingenio (field specimen; Carbajal-Márquez et al. 2021 [9]).

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