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# GEOGRAPHIC VARIATION IN SEXUAL DIMORPHISM OF BROADLY DISTRIBUTED NEOTROPICAL SNAKES: THE CASE OF *IMANTODES CENCHOA* IN LOS TUXTLAS, VERACRUZ, MEXICO

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**Abstract.**—Understanding the variation of morphological traits in a population is essential to comprehend their ecological interactions and their role in the ecosystem in a given geographic region. Here, we evaluated the sexual dimorphism of the Blunt-headed Tree Snake (*Imantodes cenchoa*) in Los Tuxtlas, Veracruz, Mexico, using data from 263 specimens sampled between 2013–2019. We found 164 adults, 74 juveniles, and 25 hatchlings. Adults were sexually dimorphic where females are larger than males in head length ( $t = 5.42$ ,  $df = 138.94$ ,  $P < 0.001$ ) and width ( $t = 4.42$ ,  $df = 142.79$ ,  $P < 0.001$ ), and weight ( $t = 2.00$ ,  $df = 131.52$ ,  $P < 0.001$ ). Our findings do not match reports from other populations within the broad geographic distribution of the species along México and Central and South America. These differences can be better attributed to differential effects of sexual selection between populations, rather than to an effect of the sampling method used. We expect our results may trigger research comparing sexual dimorphism among broadly distributed populations of tropical snakes.

**Key Words.**—arboreal snakes; Blunt-headed Tree Snake, Dipsadidae; tropical forests

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## INTRODUCTION

Sexual dimorphism (SD) can be defined as the complex of differences in phenotypic traits between females and males of a species, including ecological, behavioral, morphological, and physiological (Mori et al. 2017; Choe 2019). The evolutionary origin of sexual dimorphism was proposed by Darwin (1859) in light of sexual selection and ecological divergence. Since then, studies in the main groups of vertebrates, such as amphibians, reptiles, birds, and mammals, have analyzed the sources of SD at different levels, from genetics to ecology (e.g., Zarkower 2001; Ceballos and Valenzuela 2011; Murray et al. 2021).

Morphological variation is one of the main traits where SD can be observed (Loebens et al. 2019). Differences between females and males in body size (Carfagno and Waterhead 2006; Hyslop et al. 2014), coloration (Stuart-Fox and Ort 2004), shape (De Fuentes-Fernández et al. 2019), and use of resources (Camilleri and Shine 1990; Luiselli 2006) are common among vertebrates. Changes in the shape and size of some structures may maximize the use of certain

characters in intrasexual competition (e.g., male to male), or even avoid intersexual competition in the use of resources (male vs. female), therefore enhancing the fitness of a population (Bonnet et al. 1998; Shine 1994). Understanding the segregation of morphological traits between sexes is essential to comprehend the main ecological aspects of any species.

Among reptiles, the SD of snakes has been well-studied. In snakes it is typically observed in snout-vent length (SVL), tail length (TAL), SVL/TAL proportions, weight (W), shape, and head proportions (width vs. length; King 1989; Shine 1994). Because reproductive success in males and females is determined in different ways, it is expected that sexes will differ not only in outstanding morphological traits (e.g., body size or length) but in other more inconspicuous aspects of their shape and form (Bonnet et al. 1998). Snakes offer a comprehensive model for the analysis of SD due to the presence of morphological traits independent of sexual selection. Many morphological features such as limbs, head, or jaw are not directly involved in the mating process, unlike other conspicuous traits in vertebrates influenced by sex. Some examples of these traits are



FIGURE 1. (A) Blunt-headed Tree Snake (*Imantodes cenchoa*). (B) Lateral view of the head. (C) Dorsal aspects of the head. All specimens are from Los Tuxtlas Region, Veracruz, Mexico. (A photographed by Leo Fernández Badillo and B, C by Eric Centenero Alcalá).

coloration or the mating process, which may directly favor morphological differences between the sexes.

Here, we analyzed sexual dimorphism in a population of the Blunt-headed Tree Snake (*Imantodes cenchoa*; Fig. 1) in Los Tuxtlas Biosphere Reserve, Veracruz, Mexico, addressing three questions. Does SD exist in this population? If present, in what traits is it possible to observe SD? Is the observed pattern of SD the same as for other populations of *Imantodes cenchoa* throughout its distribution in Central and South America? According to the evolutionary theory of SD in snakes, we expect to find differences in morphological traits between sexes with larger (SVL) and heavier (body weight) females as seen in other species of neotropical colubrids.

#### MATERIALS AND METHODS

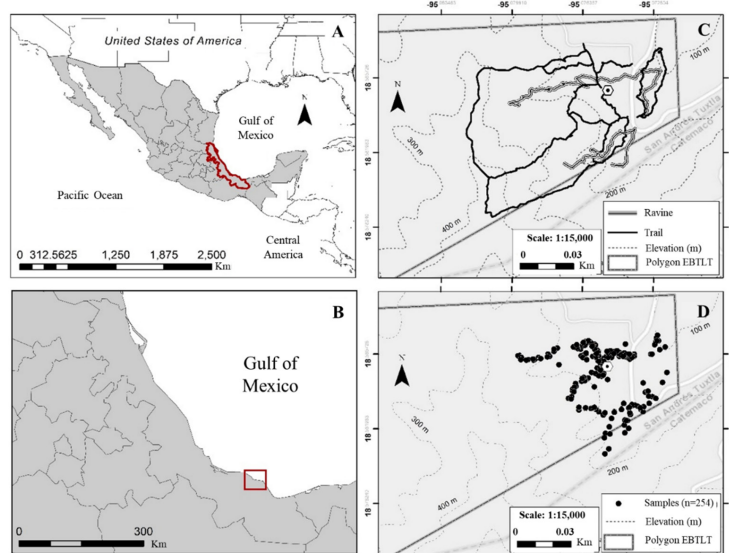
**Study species.**—The Blunt-headed Tree Snake (Colubridae: Dipsadinae) is widely distributed from Mexico to Argentina. It is a long and slender snake with an adult average total length of 700 mm, although some specimens may exceed 1,000 mm (Pérez-Higareda et al. 2007). It is reported that this species generally rests on branches of palms or bromeliads and moves along shrubs or small trees, or on the forest litter where vegetation is dense (Henderson and Nickerson 1976; Álvarez del Toro 1982; Muñoz-Alonso et al. 1992; Pérez-Higareda et al. 2007). In Los Tuxtlas, however, it is mostly found in shrubs close to the ground at night (unpubl. data).

Hatchlings are born with a minimum total length of 232 mm and are considered juveniles from 327 mm to 450 mm, although there may be variation in the time of sexual maturity throughout its distribution (Zug et al. 1979; de Sousa et al. 2014). In Los Tuxtlas, minimum SVL at maturity was 450 mm (Tepos et al. 2021). Therefore, it is considered that in this region of Mexico, adults mature sexually at a shorter length compared to other localities.

**Study area.**—We sampled snakes at Research Lot 67 of Estación de Biología Tropical Los Tuxtlas (EBTLT) of the Instituto de Biología, Universidad Nacional Autónoma de México (18.584900°N, -95.073932°E; WGS 84; 148 m elevation; Fig. 2). The EBTLT is located within Los Tuxtlas Biosphere Reserve at the eastern slope of the core zone of the San Martín volcano, 30 km northeast of Catemaco, Veracruz (Figueroa and Chontal 2017). Research Lot 67 covers 149.53 ha that are easy to access and survey along well-marked trails.

Los Tuxtlas region is dominated by Tropical Rainforest and represents the boreal extreme distribution for this type of vegetation and one of the last remnants of large-scale Tropical Rainforest in Mexico (Torres-Orozco et al. 1997). The temperature of the Los Tuxtlas region ranges from an average of 13° C in February to 35° C in May, with an annual average of 22° C (Soto and Gama 1997). Precipitation ranges from 60 mm during the dry season between March and May to 4,959 mm during the rainy season between June and February (Soto 2004). In the landscape there are constant interruptions of the terrain, generating an elevational gradient that ranges from 150 to 700 m forming steep slopes and streams with areas devoid of shrub vegetation due to the complex orography of the landscape.

**Sampling method.**—We collected data from 2013 to 2015 during rainy and dry seasons. We conducted surveys for two weeks every month following established transects on trails and in streams (Fig. 2). Subsequently, during the rainy season in June and July 2018 and 2019, a period in which *I. cenchoa* has its peak of activity, we completed two intensive surveys accumulating approximately 62 effective sampling days for both seasons. Because *I. cenchoa* is nocturnal, we surveyed transects at a night starting at 1900 and ending at 0200 the next day. Two individuals conducted each survey accumulating 3,388 person-hours. We



**FIGURE 2.** Location of the Estación de Biología Tropical Los Tuxtlas (EBTLT) in the state of Veracruz, Mexico (A) and within Veracruz (B). Lot 67 of EBTLT showing main trails and streams within EBTLT (C). Collecting points of Blunt-headed Tree Snakes (*Imantodes cenchoa*) between 2013–2019 (D).

used Visual Encounter Surveys (Foster 2011), and we captured and measured all observed snakes recording all the microhabitats where snakes were seen. We made all measurements in situ immediately after capture and released the specimens shortly thereafter.

**Morphometric characterization.**—We described morphometrical variation of all captured specimens by measuring the head length (HL) and head width (HW), snout-vent length (SVL), tail length (TAL), and total length (TL) using a vernier caliper (Surtek, El Salto Jalisco, México) and a tape measure (Truper, Ciudad de México, México). We measured weight using a digital balance (OHAUS, Ciudad de México, México) to 0.1 g. To establish age classes, we followed the criteria of Zug et al. (1979) to separate hatchlings from juveniles and Tepos-Ramírez et al. (2021) to separate juveniles from adults. Based on previous information, we considered hatchlings to have  $SVL < 327$  mm, juveniles  $327 < SVL < 450$  mm, and adults  $SVL > 450$  mm. For sex determination, we used hemipenis eversion for adults and sexing probes for hatchlings. (Data are available in Mendeley <https://data.mendeley.com/datasets/vj965x7jvc/1>).

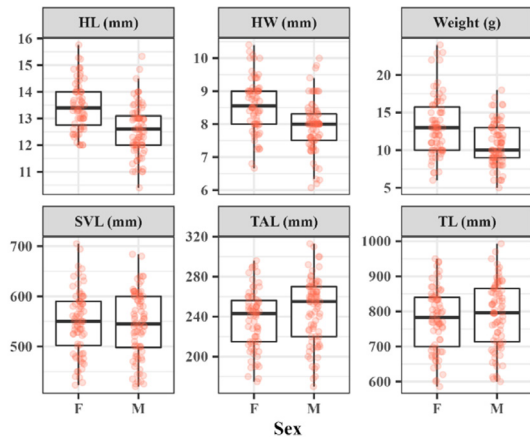
**Statistical analysis.**—When necessary, we tested the data for normality and homogeneity of variance. We used a Student’s *t*-test to compare morphological data among sexes and establish traits with sexual dimorphism among adults (Zar 2010). We used a Chi-Square Test for differences in sex ratios. We only performed statistical analysis on information gathered from adults to avoid extreme ontogenetic variation. To establish significant differences between groups (age class and sex), we performed a one-way Analysis of Variance (ANOVA) to determine which variables have a significant effect on differences between groups. All analyses were done using R software version 4.1.2 (R Core Team 2018) with  $\alpha = 0.05$ .

## RESULTS

We caught 263 specimens: 164 adults, 74 juveniles, and 25 hatchlings, of which 143 were females and 120 males. There was a proportional increase in measurements associated with age classes (Table 1). We observed significant differences between age classes in HL ( $F_{2,245} = 145.4$ ;  $P < 0.001$ ), HW ( $F_{2,245} = 103.5$ ;

**TABLE 1.** Morphological traits of Blunt-headed Tree Snakes (*Imantodes cenchoa*) from Los Tuxtlas Biosphere Reserve, Veracruz, Mexico are grouped by sex and all lengths are shown in millimeters and weights in grams. In each case, the mean followed by the standard deviation is shown in the first row, and the maximum and minimum values of each measurement for each classification are indicated in parentheses. Abbreviations are SVL = Snout-vent length, TAL = Tail length, TL = Total Length, HL = Head length, and HW = Head width.

	SVL (mm)	TAL (mm)	TL (mm)	HL (mm)	HW (mm)	Weight (g)
Females	463.42 ± 124.38 (705–430)	184.02 ± 69.46 (329–130)	651.72 ± 184.00 (1023–586)	12.39 ± 2.07 (19.30–7.72)	7.96 ± 1.30 (12.30–7.72)	10.09 ± 5.43 (24–1.50)
Males	462.31 ± 133.73 (684–454)	189.90 ± 80.23 (326–190)	667.44 ± 199.07 (998–652)	11.69 ± 1.73 (19.50–7.81)	7.40 ± 1.06 (10–7.81)	8.31 ± 4.32 (18–1)



**FIGURE 3.** Tukey diagram showing the significant differences in head length (HL), head width (HW), and weight between age classes of morphological traits of Blunt-headed Tree Snakes (*Imantodes cenchoa*) from Los Tuxtlas Biosphere Reserve, Veracruz, Mexico. The traits snout-vent length (SVL), tail length (TAL), and total length (TL) did not differ significantly between sexes.

$P < 0.001$ ), and weight ( $F_{2,246} = 179.3$ ;  $P < 0.001$ ). Otherwise, measurements of head lengths and weight were variable, and HL and HW values overlapped in the extreme measurements among the three age classes, with juveniles sometimes having head sizes equal to those of adults (Fig. 3). In the juvenile-adult transition, it was possible to observe a substantial change in average weight from 228 g in juveniles to 262 g in adults.

The maximum TL for females (1,023 mm) was 2.5% greater than males (998 mm; Table 1). On average, SVL of females was 0.3% higher compared to males, and the heads of the females were 5.7% longer and 7.1% wider than the males. Females were also 17.7% heavier than males, on average. In contrast, the average TL and TAL was 2.4% and 3.1% longer in males compared to females, respectively; however, none of these differences were significant. Females showed broader ranges of variation in SVL, TAL, and TL with respect to males (Table 1).

We found significant sexual dimorphism in HL, HW, and weight (HL:  $t = 5.42$ ,  $df = 138.94$ ,  $P < 0.001$ ; HW:  $t = 4.43$ ,  $df = 142.79$ ,  $P < 0.001$ ; weight:  $t = 2.00$ ,  $df = 131.52$ ,  $P = 0.040$ ), indicating that the females possessed longer and wider heads, and are heavier than males. SVL ( $t = 0.361$ ,  $df = 146.87$ ,  $P = 0.712$ ) and TL ( $t = -0.654$ ,  $df = 146.97$ ,  $P = 0.513$ ) were not significantly different between sexes, but we found significant differences in TAL ( $t = -1.95$ ,  $df = 14.37$ ,  $P = 0.052$ ), with males having longer tails than females (Fig. 3). The sex ratio (120 males:143 females) was not significantly different from 1:1 ( $\chi^2 = 2.011$ ,  $df = 1$ ,  $P = 0.156$ ).

## DISCUSSION

**Morphological traits in sexual dimorphism.**—Female *I. cenchoa* from Los Tuxtlas possessed heavier

bodies and larger heads in comparison to males. We found a significant difference in weight increase in individuals larger than 450 mm. This weight increase can be caused by the formation of the egg after mating season only in sexually mature pregnant females. Interestingly, the increment of weight after reaching 450 mm coincides with the minimum size at maturity previously reported by Tepos et al. (2021). Weight differences between sexes are well documented in many other snake species such as the Green Whip Snake (*Hierophis viridiflavus*), the Aesculapean Snake (*Zamenis longissimus*), the Common Garter Snake (*Thamnophis sirtalis*), and the Asp Viper (*Vipera aspis*), where the reproductive role seems to favor the development of female structures associated with energy processing and storage such as the alimentary tract, liver, and fat stores (Bonnet et al. 1998; Krause et al. 2003). These differences, however, are not always reflected in total weight. Changes in weight in mature pregnant females throughout the year from egg development until deposition needs to be evaluated. Heavier bodies in males can be associated with a scramble mating process; nevertheless, there is only one report of aggregation from Perú (Doan and Arriaga 1999) that may represent a hint of a scrambling mating process in *I. cenchoa*. This information needs to be evaluated locally at Los Tuxtlas, especially if we consider other records of male-male combat associated with the mating process in Pará, Brazil (Santos-Costa and Prudente 2005) and Napo, Ecuador (Thomas 2019). In this process males with greater weight and length are favored (Shine 1994), which may indicate that in the study area, sexual competition may be a weak selection pressure.

In Los Tuxtlas, *I. cenchoa* females possessed significantly longer and wider heads than males. Results were similar to those observed for *I. cenchoa* in the Amazon region in Brazil (de Sousa et al. 2014). These differences may be the result of a strategy to maximize foraging efficiency by avoiding intersexual competition for food, as suggested for *Thamnophis sirtalis* (Shine and Crews 1998), the Colubrine *Laticauda colubrina* (Shine et al. 2002), and the Northern Cottonmouth *Agkistrodon piscivorus* (Vincent et al. 2004). This hypothesis does not apply to *I. cenchoa*, nevertheless, because no differences in feeding preferences between sexes or even ontogeny were observed in the Amazon population where all individuals feed mainly on the Slender Anole (*Anolis fuscoauratus*; de Sousa et al. 2014). In Los Tuxtlas, the true feeding habits of *I. cenchoa* are unknown, as no data on feeding or stomach contents have been reported.

Throughout the distribution of *I. cenchoa*, populations may or may not show SD and, if present, differences can be observed in many morphological traits (Appendix Table 1). A detailed study is needed to determine if the observed differences represent a common pattern among snakes or an isolated trait

in this snake, either due to phenotypic plasticity or selection pressures. The lack of SD of SVL in Los Tuxtlas population contrasts with the findings of de Sousa et al. (2014), who reported that female *I. cenchoa* have SVL significantly longer than males in Amapá, Amazonas, Maranhão, Pará, and Rondonia in the Brazilian Amazon. To the contrary, Pizzato et al. (2008a) reported males to be larger than females in their mean size in the south and southeast of Brazil. Zug et al. (1979), in his review, however, did not report SVL comparisons between sexes for the populations of Costa Rica (Río Frio), Ecuador (Santa Cecilia, Limoncocha, and Río Bobonaza), Honduras (Ulúa R. and Portillo), México (Escuintla, Panamá (canal zone), and Perú (Iquitos). Differences in weight, but not in SVL, can be associated with better body condition for the Los Tuxtlas female population.

As in Los Tuxtlas, *I. cenchoa* tail length was not sexually dimorphic in Amapá, Amazonas, Maranhão, Pará, and Rondonia (Brazil), in the canal zone (Panamá), Santa Cecilia (Ecuador), or Iquitos (Perú; de Sousa et al. 2014; Zug et al. 1979). Males with slightly longer tails than females, however, were reported in northern populations from Escuintla (Chiapas), Yoro (Honduras), and Heredia (Costa Rica), and, interestingly, in the southeast region of Brazil, from Minas Gerais to Santa Catarina (Zug et al. 1979; Pizzato et al. 2008a). An increase in tail size is usually associated with an increase in length of the hemipenes (Shine et al. 1999), but this correspondence is not known for the studied species.

Sexual dimorphism in snakes has also been observed in several Neotropical snakes on the American continent. Larger females are the norm in the Military Ground Snake (*Erythrolamprus miliaris*), Neuwied's False Fer-de-lance (*Xenodon neuwiedii*), and Wagler's Snake (*Xenodon merremii*) from Brazil (Pizzato and Marques 2006; Pizzato et al. 2008b). The main hypotheses to explain SD suggest that it may be the result of inter- and intrasexual competition, where the availability of food resources or the possibility of reproduction are determinant factors for this process (Shine 1994). The biological reasons underlying SD in *I. cenchoa* in Los Tuxtlas, however, remain unknown.

It has been reported that in Los Tuxtlas, *I. cenchoa* may feed primarily on hylid frogs and anole lizards (Vogt 1997). During the rainy season, small arboreal lizards like the Lesser Scaly Anole (*Anolis uniformis*), Silky Anole (*A. sericeus*), Greater Scaly Anole (*A. tropidonotus*), and the Collared Dwarf Gecko (*Sphaerodactylus glaucus*), and the ground-dwelling nocturnal frogs like the Common Leaf-litter Frog (*Craugastor loki*), Volcan San Martin Rainfrog (*C. vulcani*) and Elegant Narrowmouth Toad (*Gastrophryne elegans*), are very abundant (Urbina-Cardona et al.

2006; Cabrera-Guzmán y Reynoso 2012); however, SD can be multifactorial and elements such as divergence in food preferences or habitat use can lead to intrapopulation morphological changes (Vincent et al. 2004; Mori and Vincent 2008). Differences in food habits among sexes and its potential to affect SD need to be explored further.

We found a 1:1 sex ratio, although de Sousa et al. (2014) and Zug et al. (1979) found a male-biased sex ratio from different localities along the *I. cenchoa* distribution. Our sample size in Los Tuxtlas is the largest ever studied, where all the specimens come from the same locality and within a relatively small area. We believe that differences in sex ratios reported by Zug et al. (1979) and de Sousa et al. (2014) may be skewed because the data come from scattered populations.

*Imantodes cenchoa* is a species with a wide distribution and it is expected that life-history features among populations are not necessarily shared as each population is subjected to different selection pressures. We believe that differences in male and female traits throughout the different populations respond better to real variation in SD associated with effects of sexual selection at each site, although it also may be an effect of sample size. For example, the results of Zug et al. (1979) and Pizzato et al. (2008a) are based on only 33 and 36 specimens from different localities, respectively. In contrast, our large sample size from Los Tuxtlas, which shows statistically reliable results, can be a framework for further studies about SD. With the exception of chelonians, differences in SD among reptile populations of the same species have been rarely reported (Zamudio 1998; Blanckenhorn et al. 2004; Diaz de la Vega-Perez et al. 2019; Forsman 2019). We expect our findings will encourage research comparing sexual dimorphism among broadly distributed populations of tropical snakes.

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**APPENDIX TABLE 1.** Morphometrics analyzed by different authors to characterize the sexual dimorphism of the Blunt-headed Tree Snake (*Imantodes cenchoa*). The average values are followed by the standard deviation for both sexes is shown when available. All measurements are in mm. Abbreviations are SVL = Snout-vent length, TAL = Tail length, TL = Total Length, HL = Head length, and HW = Head width. One asterisk (\*) indicates that TAL is presented as a proportion (%) of the total length and two asterisks (\*\*) indicate that the authors only reported lengths from three specimens from Chiapas, México. The sex of the individuals used in the analysis is unknown.

	n (F,M)	SVL		TAL		TL		HL		HW		Location
		Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	
Myers (1982)*	78 (38,40)	–	–	–	–	–	–	–	–	–	–	Boca del Toro, Panamá
Zug et al. (1979)**	33 (33,?)	715.90 ± 67.70	–	–	–	–	–	–	–	–	–	Costa Rica, Ecuador, Honduras; México and Perú
Pizzato et al. (2008a)*	36 (18,18)	–	–	771.20 ± 67.90	764.2 ± 95.00	347.00	362.40	–	–	–	–	Southeast Brasil
De Sousa et al. (2014)	121 (71,1,50)	731.53 ± 67.84	690.60 ± 70.86	731.53 ± 67.84	690.6 ± 71.86	333.60 ± 35.97	311.2 ± 38.7	14.04 ± 1.00	12.78 ± 0.99	2.21 ± 0.09	2.07 ± 0.08	Amazonas, Brasil
This study	230 (119,111)	463.42 ± 124.38	462.31 ± 133.73	449.30± 128.40	460.50 ± 130.50	188.40 ± 64.00	204.1 ± 65.7	12.10 ± 2.10	11.90 ± 1.70	7.78 ± 1.24	7.35 ± 1.07	Los Tuxtlas, México