

Characterisation of sexual dimorphism and male colour morphs of *Tropidurus semitaeniatus* (Spix, 1825) in three populations from northeast of Brazil

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Abstract. Sexual dimorphism, including dichromatism, is a strong indicative of past or ongoing processes of sexual selection, which can also promote discrete variants within a sex. These variants can be either in terms of morphology, colouration, physiology, and behaviour, such as colour morphs with alternative mating tactics. However, as sexual selection acts in a populational level, distinct populations might be under different selection pressures conferring distinct levels of dimorphism and distinct number, and frequencies, of morphs in the cases in which it occurs. The Striped Lava Lizard, *Tropidurus semitaeniatus*, is a small ($\leq 14\text{g}$) flat lizard inhabitant of rocky outcrops distributed throughout all the semi-arid Caatinga biome in Brazil. Two discrete colour morphs were described within adult males from a single population, but their function, presence, frequencies, and morphological differences are still unexplored, especially among populations. Here, with a sample of 343 individuals, we present comparative data of morphometry and relative frequencies of sexes and both male colour morphs of *T. semitaeniatus* among three distinct populations from the State of Rio Grande do Norte, Brazil. Relative frequencies of male morphs differed substantially among populations. Male morphs are dimorphic in body size only within the population with equal relative morph frequencies, while the remaining populations have opposite morph-biased frequencies. Our results suggest that populations are under distinct selection pressures, which should be explored in future behavioural studies addressing intra and intersexual interactions between male morphs.

Keywords. Striped Lava Lizard, alternative reproductive strategies, dichromatism, secondary sexual trait, interpopulational variation, morph frequencies, body size

Introduction

Sexual dimorphism, different phenotypes between sexes of a species, is described in several groups of animals (e.g., Cullum, 1998; Isaac, 2005; Pinto et al., 2005). There are many different hypotheses to explain

it, including mechanisms that relate sexual dimorphism to gamete investment or anisogamy (Wells, 2007), resource partitioning or availability (Schoener, 1967), sexual selection (Olsson et al., 2002), species' life history (Andersson, 1994), and phylogeny (Isaac, 2005).

Among the examples of sexual dimorphism known in mammals, birds, amphibians and reptiles, differences in body size, morphology, behaviour, and colouration are described (e.g., Fairbairn et al., 2007). In squamate reptiles, most reports of sexual dimorphism are in body size and coloration (Vitt and Cooper, 1985; Pinto et al., 2005). Within the genus of lizards *Tropidurus*, in addition to sexual dimorphism in body size, colour differences are reported for several species (Vitt, 1993; Van Sluys, 1998; Pinto et al., 2005). Also, distinct colour morphs within adult males are known for *Tropidurus semitaeniatus* (Spix, 1825) (Ribeiro et al., 2010).

Tropidurus semitaeniatus has two male colour morphotypes, occurring often in sympatry: the coloured patches in the pre-cloacal flap and ventral thighs common in Tropiduridae males can be either Yellow,

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or Black (Ribeiro et al., 2010). Females do not exhibit such coloured patches, and neither do juveniles nor subadults (personal observation). So, coloured patches seem to be a secondary sexual trait as it is developed only when male individuals reach sexual maturity. Adult males' dorsal coloration is apparently (according to human vision) homogeneous. However, there are evidences suggesting that lizards are able to visually distinguish sexes and male colour morphs even on dorsal colorations (Bruin   et al. in press). Despite these interesting patterns, colour variation on the patches of *T. semitaeniatus* is reported only from a single population (Ribeiro et al., 2010). Issues of variations among different populations are thus still unknown. Both composition and relative frequencies of different morphs of polymorphic systems are fundamental information to understand whether polymorphism is widely distributed or a particular pattern of a single population. In addition, morphological differences (such as body size and other morphometric measures) between colour morphs are also of a particular interest for behavioural, and evolutionary ecology studies. For instance, body size is known to influence female choice in lizards (Van Sluys et al., 2002). Also, differences in lizards' limb length are known to vary according to microhabitat use (Losos et al., 1998).

Information of occurrence, composition, frequency, and variation of multiple morphotypes among populations are important for studies on several areas, ranging from behavioural ecology to evolutionary dynamics on alternative reproductive strategies (Sinervo et al., 2007). Our goal was to characterize the composition (which morphs are present) and identify whether there are differences in morphometry and relative frequencies of sexes and male colour morphs among three populations of *T. semitaeniatus*.

Materials and Methods

We collected lizards from three populations (Figure 1a) within the Caatinga biome, located in Rio Grande do Norte State at municipality of Jo   C  mara (JC) (Lat: -5.535209, Long: -35.815176), Lagoa de Velhos (LV) (Lat: -6.007682, Long: -35.871824) and Jucurut   (JU) (Lat: -6.035178, Long: -37.018430). Regional climate is characterized as BsWh, which is a semi-arid climate with a marked rainy season starting at the end of the summer (by late April), according to Koeppen (Alvares et al., 2013). Vegetation is characterized as hyperxerophytic (Andrade-Lima, 1981). We sampled the lizards actively by noose or hand between 08:00

and 17:00 h, between January and February of 2015, and between December of 2015 and January of 2016. Total sampling hours in the localities of JC, JU and LV were 144, 120 and 90 hours respectively (9 h per day per researcher).

We classified lizards as juveniles or adults based on their morphological traits. Juveniles and adults express distinct patterns of colouration, including ventral coloured patches that are solely expressed in adult males and are thus a classifier of sex and maturity of the lizards (Figure 1b). It is known through previous histological analysis of the species that the minimum size (in snout-to-vent length, SVL) for females to be reproductively mature is 59 mm and for males the minimum size is 68.5 mm (Ribeiro, Silva, and Freire, 2012). Thus, we first checked for ventral coloured patches to identify adult males. From the remaining individuals we measured SVL and identified as juveniles the individuals smaller than 59 mm SVL. We sexed the unpatched individuals bigger than 59 mm SVL by manually exposing the hemipenis. We then measured the following morphometric variables: snout-to-vent length

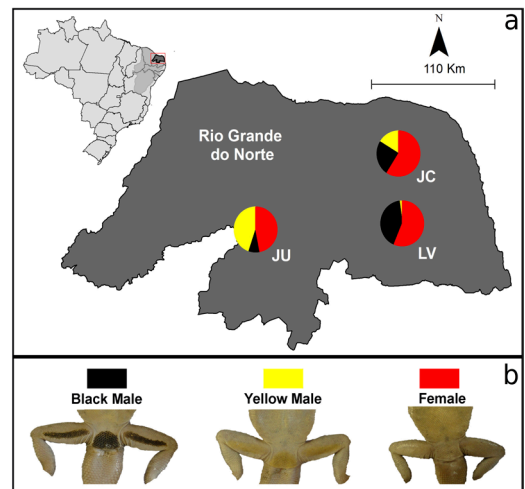


Figure 1. Study sites in the municipalities of Jucurut   (JU), Jo   C  mara (JC) and Lagoa de Velhos (LV), in the State of Rio Grande do Norte, Brazil, with the relative proportions of *Tropidurus semitaeniatus* adult individuals per population (a). Ventral view of the lizards showing femoral and pre-cloacal flaps (b) of Black male colour morph (left, in black), Yellow male colour morph (centre, in yellow), and female (right, in red). Adult females do not express ventral coloured patches. Distribution of the Caatinga biome is shown in medium grey in northeast region of Brazil (top-left).

(SVL), body width (BW) measured at the wider portion of the thorax, body height (BH) measured at the higher part of the thorax; head width (HW) and head height (HH) measured at the wider and higher portions of the head, respectively. We measured head length (HL) from the snout to the beginning of the auricular cavity, foreleg length (F), hindleg length (H) and tail length (TL). We used a digital calliper with precision of 0.01 mm in our length measurements. We classified males according to their colour morphs (two morphs: yellow or yellow-and-black) that are expressed in their pre-cloacal flap and ventral thighs (Ribeiro et al., 2010), hereafter referred solely as Yellow males and Black males, respectively. After the measurements, we released the lizards at each sampling location.

For the morphometric characterization of each population of the species we calculated mean and standard deviation of the linear morphometric variables (SVL, BW, BH, HW, HH, HL, F, H, TL) of juveniles, males and females. We also characterized both colour morphs' (Black and Yellow) mean and standard deviation of morphometric variables for each population. In order test for body size differences of sexes and morphs among and within populations we first calculated a single variable BS from the linear morphometric measures SVL, BW, BH, HW, HH, HL, F, and H (we did not use tail length due to possible previously autotomized and regenerated tails). To meet requirements of normality to compose the variable, we log-transformed (base 10) all morphometric variables. Then, we composed BS as an isometric size variable following the protocol of Somers (1986): We calculated an isometric eigenvector of p variables with all coefficients equal to $p^{-0.5}$ (Jolicœur, 1963) and obtained the isometric size-adjusted variables by multiplying the $n \times p$ matrix of log-transformed morphometric data by the isometric eigenvector. Thus, BS is a composed variable that represents overall body size of lizards that accounts for all linear morphometric variables and not solely on SVL. Then, to access whether there are differences in body size between sexes and among populations we performed an ANCOVA with BS as dependent variable, and sex and population as factors in the model. Similarly, to test for differences in body size of males among populations and between male colour morphs we performed an ANCOVA with BS as dependent variable, and colour morph and population as factors. We considered as significant the analysis yielding a p value below 0.05. Further, we performed Tukey-tests to access pair wise comparisons. To characterize occurrence of male colour morphs among populations we determined frequency of occurrence of

morphs of each population and tested such proportions with Chi-squared tests. We ran all analyses in R *software* (R Core Team, 2015).

Results

From our total sample size ($n = 343$ lizards), we identified 16 juveniles and 327 adults. Among sexed adult individuals, we identified 156 females and 171 males. The population with most individuals was JC with 246 (16 juveniles, 124 males and 106 females), followed by JU with 49 individuals (26 males and 23 females) and LV with 48 individuals (21 males and 27 females) (Table 1; Figure 1a). Juveniles varied between 44.32 and 59 mm (mean 55.29 ± 4.29) in their SVL. Females varied in their SVL from 54.64 to 76.3 mm (mean 67.07 ± 0.36) and males' SVL varied between 59.0 and 88.2 mm (mean 74.4 ± 5.28). Black males' SVL varied between 68.0 and 88.2 mm (mean 78.41 ± 4.13), while Yellow males varied between 59.0 and 87.7 mm (mean 73.65 ± 5.46) (Table 1).

From our full sample, males and females differed in body size (BS) ($F_{1,261} = 403.52, p < 0.0001$). Sexual dimorphism in body size was present within all populations (Tukey HSD, $p < 0.0001$ for JC, JU and LV). Both males and females differed in body size among some populations in within-sex comparisons ($F_{2,261} = 17.89, p < 0.0001$). Further Tukey tests indicated that males from LV differed from males from both JC ($p < 0.001$) and JU ($p < 0.001$) populations in body size, while males from JU and JC did not (Tukey HSD; $p = 0.99$). Females from LV also differed in body size from both JU and JC (Tukey HSD; $p < 0.0001$, and $p < 0.05$, respectively). However, females from JC did not differ from JU (Tukey HSD; $p = 0.86$).

In a comparison between male colour morphs, body size (BS) of Black and Yellow males differed ($F_{1,110} = 33.28, p < 0.0001$) in the full sample. Post hoc Tukey test showed that male morphs differ in body size within JC ($p < 0.0001$), but not within LV ($p = 0.085$), nor JU ($p = 0.99$). When comparing body sizes of each colour morph, Yellow males did not differ among populations ($F_{2,48} = 2.98, p = 0.06$), however Black males did ($F_{2,62} = 6.2, p < 0.01$). Post hoc indicated that Black males of LV differed in body size from both JC ($p < 0.01$) and JU ($p < 0.05$). Black males from JC and JU did not show significant differences in body size between the two populations (Tukey HSD; $p = 0.5$).

Among all sampled males, 55.37% ($n = 67$) were Black and 44.62% ($n = 54$) were Yellow. Within populations, JC had 57.33% of Black males ($n = 43$) and 42.66%

Table 1. Linear morphometric measures (minimum, maximum, mean, and standard deviation) of females, males, and male colour morphs (Black and Yellow) of *Tropidurus semitaeniatus* lizards sampled in three populations of the State of Rio Grande do Norte, Brazil. Measures are presented by rows referring to the populations of João Câmara (JC), Jucurutú (JU) and Lagoa de Velhos (LV). Values presented by columns refer to number of individuals sampled by population (N), snout-to-vent length (SVL), body width (BW), body height (BH), head width (HW), head height (HH), head length (HL), foreleg length (F), hindleg length (H) and tail length (TL), and are all expressed in millimetres (±SD).

Population	N	SVL	BW	BH	HW	HH	HL	F	H	TL
Female (n = 156)										
JC	106									
	Min-Max	57.9-76.3	12.5-25.3	3-11.5	8.9-12.8	3.9-8.6	12.4-16.6	29.8-41.2	37.9-60	30-128
	Mean	67.72 (±4.30)	18.35 (±2.55)	5.7 (±1.19)	11.04 (±0.75)	5.56 (±0.58)	14.63 (±0.92)	34.21 (±2.05)	48.87 (±3.02)	108.39 (±13.75)
JU	23									
	Min-Max	54.64-67.59	12.31-20.32	5.49-8.9	8.89-10.65	4.79-6.4	12.21-14.84	27.38-34.43	40.62-50.49	59-117
	Mean	62.26 (±3.48)	16.2 (±1.82)	7.09 (±1.03)	9.87 (±0.43)	5.44 (±0.7)	14.0 (±0.62)	31.25 (±1.78)	45.6 (±2.5)	97.13 (±14.4)
LV	27									
	Min-Max	61.3-72.7	14.7-22.2	4.6-9.4	9.5-12.2	4.7-6.5	13.2-15.7	29.78-36.5	45.5-54.7	29-151
	Mean	68.83 (±2.88)	18.83 (±1.78)	7.12 (±1.16)	10.82 (±0.61)	5.78 (±0.41)	14.75 (±0.58)	33.91 (±1.5)	50.9 (±2.27)	107.44 (±27.6)
Male (n = 171)										
JC	124									
	Min-Max	53.8-87.7	13-28.9	4.2-7.3	10.8-15.5	4.8-8.4	14.2-25.4	32.4-42.7	43.4-62	75-221
	Mean	76.1 (±5.60)	21.03 (±0.43)	7.81 (±8.13)	13.07 (±1.13)	6.55 (±0.74)	17.15 (±1.63)	38.5 (±2.3)	56.12 (±3.91)	126.33 (±21.41)
JU	26									
	Min-Max	59-81.8	13.47-22.81	5.5-10.2	9.36-13.95	5.82-7.5	13.28-17.8	29.89	46.21-41.6	31-140
	Mean	75.22 (±4.33)	19.36 (±2.22)	7.57 (±1.21)	12.44 (±0.84)	6.94 (±0.37)	16.95 (±0.89)	37.78 (±2.48)	56.58 (±3.38)	109.73 (±28.74)
LV	21									
	Min-Max	63.4-88.2	15.4-27.4	6.1-11.2	11.1-14.9	5.9-8.3	15.1-19.9	34.5-43.7	52.7-65.9	86-164
	Mean	78.5 (±4.93)	22.11 (±2.82)	8.2 (±1.1)	13.51 (±0.93)	7.23 (±0.61)	17.62 (±1.08)	39.6 (±2.53)	59.83 (±3.31)	133.57 (±20.61)
Male Morph: Black (n = 67) and Yellow (n = 54)										
JC										
Black	43									
	Min-Max	68-87.1	17.7-28.9	4.7-9.2	10.8-15.2	5.2-8.4	14.2-19.3	35.7-42.7	47.3-61.9	75-221
	Mean	78.35 (±4.4)	22.46 (±3.2)	6.9 (±1.1)	13.5 (±0.98)	6.8 (±0.71)	17.49 (±0.91)	39.5 (±1.8)	57.04 (±3.5)	131.58 (±21)
Yellow	31									
	Min-Max	64-87.7	14.7-27	4.2-11.4	10.8-15.5	4.8-7.5	14.3-25.4	32.4-42.2	43.4-62	77-160
	Mean	72.68 (±5.6)	18.86 (±2.56)	6.72 (±1.67)	12.42 (±1.04)	6.22 (±0.66)	16.64 (±2.25)	37.41 (±2.55)	54.73 (±4.18)	118.37 (±19.74)
JU										
Black	4									
	Min-Max	71.8-76.9	17.65-22.6	6.11-8.64	11.63-12.99	6.67-7.33	16.87-17.64	34.17-38.57	52.85-56.78	103-124
	Mean	74.7 (±2.25)	19.1 (±2.34)	7.61 (±1.13)	12.4 (±0.6)	7.02 (±0.27)	17.13 (±0.36)	37.02 (±1.95)	55.53 (±1.81)	114.5 (±9.39)
Yellow	22									
	Min-Max	59-81.8	13.47-22.81	5.5-10.2	9.36-13.95	5.82-7.5	13.28-17.8	29.89-41.6	46.21-62.8	31-140
	Mean	75.31 (±4.64)	19.41 (±2.25)	7.56 (±1.25)	12.44 (±0.88)	6.92 (±0.39)	16.92 (±0.96)	37.92 (±2.58)	56.77 (±3.6)	108.86 (±31.08)
LV										
Black	20									
	Min-Max	69.3-88.2	18.9-27.4	6.1-11.2	11.86-14.9	6.3-8.3	15.3-19.9	35.3-43.7	55.7-65.9	86-164
	Mean	79.26 (±3.6)	22.45 (±2.43)	8.17 (±1.12)	13.63 (±0.77)	7.29 (±0.55)	17.75 (±0.93)	39.85 (±2.3)	60.19 (±2.95)	135.15 (±19.8)
Yellow	1									
	Value	63.4	15.4	8.8	11.1	5.9	15.1	34.5	52.7	102

of Yellow males (n = 31) and did not differ in relative frequencies of morphs, $X^2_{(1, N=74)} = 1.94, p = 0.16$. The population of LV, however, had 95.23% of Black morph males (n = 20) and 4.77% of Yellow morph males (n = 1), while JU had 15.39% of Black males (n = 4) and 84.61% of Yellow males (n = 22). Thus, relative frequencies of morphs differed within both LV and JU populations, $X^2_{(1, N=21)} = 17.19, p < 0.0001$; and $X^2_{(1, N=26)} = 12.46, p < 0.001$, respectively (Figure 1).

Discussion

Squamate reptiles usually present sexual dimorphism of body size and often of coloration (Pinto et al., 2005). Many species of the genus *Tropidurus* show dimorphism in these traits and one species, *T. semitaeniatus*, expresses two distinct colour morphs within males (Ribeiro et al., 2010). Our results show that, among the analysed populations, *T. semitaeniatus* present a consistent sexual dimorphism in body size, and that Black male colour

morph has larger body sizes than Yellow males in one (JC) of all three sampled populations. This variation of body sizes of morphs among populations should be addressed in further studies as this trait is related to several ecological features, such as thermoregulatory performance and heat loss (Meiri, 2008), both important for lizards. Moreover, besides differences in body size, the two male colour morphs have significantly distinct frequencies of occurrence depending on the population. Interestingly, these relative frequencies might be from as low as 4.77% of males of one colour morph in one population (Yellow males in LV), to 84.6% of the occurrences of this same colour morph in another population (Yellow males in JU). In other words, relative frequencies of colour morphs among populations are not uniform. In JC, relative frequencies of colour morphs are similar. Even though Black males presented a slightly higher proportion, it is not significantly different than the number of Yellow males in the population. However, morph frequencies of LV are highly imbalanced, as we found only one individual with Yellow morph. In contrast, the majority of males from JU population were Yellow morph males. This pattern might be due to ecological differences among populations, such as microhabitat or exposure from differences in vegetation (Shine, 1989). Further studies taking into account the visual contrast of colour morphs in relation to background of different populations might address the adaptive function of these colour morphs.

In our study, body size of lizards from both sexes was similar or larger than registered for the species in other studies (Ribeiro et al., 2010, Ribeiro et al., 2011). Specifically, mean and maximum SVL of females was larger than previously reported. For adult males, regardless of colour morph, mean SVL was similar to the previously registered whereas maximum SVL was superior (Ribeiro et al., 2010, Ribeiro et al., 2011). Minimum and mean SVL of juveniles were larger than the values found by Ribeiro and collaborators (2010). When analysing males of different colour morphs between studies, both morphs had higher minimum and maximum SVL than already registered, whereas mean SVL showed similar, or lower, values than already registered (Ribeiro and Freire, 2010, 2011; Ribeiro, Kolodiuk, and Freire, 2010). This result suggests that variance in body size of the populations analysed in the present study tends to be wider, while samples from the aforementioned studies showed more homogeneous values.

The body size differences among populations reported

here, in relation to other studies, might be related to sample sizes (number of individuals) that were analysed in each of the studies (343 in this study compared to 83 reported in Ribeiro et al. 2010). This is because the greater the sample size, the greater the representation of each class within samples. However, biotic interactions (e.g., predation, reproductive behaviour, or resource availability) and abiotic interactions (e.g., environmental temperature, precipitation, and luminosity) might also be affecting differences in body size among populations (Anderson and Vitt, 1990; Pinto et al., 2005).

The difference of body size between colour morphs appears to be a pattern of the species in populations with both colour morphs, with Black males presenting greater body sizes than Yellow ones (Ribeiro et al., 2010). This pattern might influence the propagation of this phenotype; as females tend to prefer larger males (Van Sluys et al., 2002; Pinto et al., 2005). Reproductive behaviour and the relation of it to male colour morphs of *T. semitaeniatus* is, however, still unclear. Further studies, especially *in situ* observations, could address this issue in order to clarify whether reproduction in this species is affected mainly by female mate choice or intrasexual competition within males. In addition, larger males also have advantages in disputes over territory, food, and agonistic encounters (Cooper and Vitt, 1988; Anderson and Vitt, 1990; Watkins, 1998).

Furthermore, our results indicate that individuals from different populations of *T. semitaeniatus* may vary in average body size. We found interpopulational variation in the BS of both females and males. Within males however, and in accordance to previous studies (Ribeiro, Kolodiuk, and Freire, 2010), colour morphs tend to differ in body size, with Black males being larger. This difference was, however, found in just one (JC) of all populations sampled, which is the single population that morphs do not differ in relative frequencies. Nonetheless, we show that male colour morphs have distinct relative frequencies among populations. Also, that *T. semitaeniatus* does not appear to have a pattern of relative abundance or frequency of a determined colour morph. Both male colour morphs had higher (e.g., Black males in LV) and lower (e.g., Black males in JU) relative frequencies in different populations. Thus, frequencies of colour morphs appear to be influenced by ecological factors, some of which could be addressed in further studies accessing crypsis against lizards' inhabiting backgrounds, vegetation cover, environmental temperatures, and thermophysiological differences between colour morphs.

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