

Sexual dimorphism in *Rhinella major* (Anura: Bufonidae) from eastern Brazilian Amazonia

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Abstract. Intersexual morphological differences within a species may occur in body size or shape. It reflects the effects of distinctive selective pressures acting differently upon males and females. Sexual selection and differences in life-history strategies between sexes can generate sexual dimorphism in anurans. Considering the relevance of morphological variation studies to provide in-depth knowledge about species and populations, we investigated sexual dimorphism in the toad *Rhinella major*. Based on 15 measurements of external morphology related to body size and shape, cluster analyses (PCA and Random Forest) and multivariate analysis of variance showed that females were larger than males in SVL. Most of the variation was tied to body size ($F_{(1,41)} = 19.07, p < 0.001$). Non-significant differences in shape were found. Our analysis points out the necessity of further investigations on the life-history aspects of *R. major* to understand the role of sexual (e.g., female fecundity) and natural selection (e.g., niche segregation) in explaining the intrasexual divergence in external morphology of this species.

Keywords: external morphology, shape dimorphism, head morphology, sexual selection, natural selection.

Sexual dimorphism is a widespread phenomenon in sexually reproducing dioecious organisms. Animals can be sexually dimorphic in several features such as body size, shape, color, physiology, and behavior (Duellman & Trueb 1994, Monnet & Cherry 2002). These dimorphic traits can be a result of both reproductive and non-reproductive microevolutionary processes (Katsikaros & Shine 1997) and most commonly evolve as size dimorphism, shape dimorphism, or the dependence of shape on size (i.e., allometry) (Vitt & Cooper 1985, Fairbairn 1997, Birch 1999).

In anurans, approximately 90% of the studied species exhibited sexual size dimorphism (Duellman & Trueb 1994, Shine 1979). Females usually exceed males in body size (Snout-Vent Length), traditionally viewed as a consequence of selection for increased fecundity (Woolbright 1983). Besides sexual size dimorphism, the intersexual differences in the shape of morphological structures have also received increasing attention as it offers a more precise morphological description of sexual dimorphism (Monnet & Cherry 2002, Berns 2013, Arantes et al. 2015, Petrović et al. 2017).

Several studies have described sexual dimorphism in anurans' head size or shape size (e.g. Arantes et al. 2015, Petrović et al. 2017, Melo-Moreira et al. 2021). However, many species are still unexplored in terms of sexual dimorphism, especially from Amazon (Garda et al. 2006, Bernarde & Kokubum 2009, Martins & Menin 2021, Santana et al. 2021). Therefore, since morphological variation studies are extremely relevant to providing in-depth knowledge about species and their populations, it is extremely relevant to include sex as a biological factor of intrinsic interest to explain morphological variation.

Rhinella major is a small-sized bufonid species, a member of the *R. granulosa* group with the widest distribution. It is distributed from the Chaco region of Bolivia to the eastern Brazilian Amazon. It is widespread in open forests through the rivers Beni, Madeira, and Amazon (Frost 2021). In Amapá state, northern Brazil, *Rhinella major* is only found in forest fragments within urban landscapes (Pedroso-Santos & Costa-Campos 2021), which makes this toad a representative

faunal element of anthropogenic environments. Adult male snout to vent lengths range from 35.8 to 75.8 mm, while females range from 33.9 to 81.1 mm (Narvaes & Rodrigues 2009). These toads are characterized by a dorsum with close or spread dark spots, resembling a mosaic pattern, with a cream-colored and non-pigmented belly (Narvaes & Rodrigues 2009). Here, we investigated intersexual disparities in morphometric characters related to body size and shape size in *Rhinella major*. This will provide an important basis for a better understanding of sexual dimorphism in this species.

We collected toad specimens from January to June 2019 in a secondary forest in the surroundings of the Universidade Federal do Amapá, Amapá, northern Brazil (00°00'S, 51°04'W). The sample area comprised a 90-ha forest fragment affected by a high anthropic disturbance in the last decades, which is in the process of secondary succession, ranging from savanna to forest formation (Figueiredo et al. 2020). We collected individuals of *R. major* during an extensive anuran inventory. We collected all individuals by hand from 19:00 to 23:00 h. Fieldwork was conducted on three consecutive nights each month. Males were located by active searching, based mostly on auditory surveys, while females were collected opportunistically through active visual searching. We euthanized the collected specimens using 5% lidocaine, fixed them in 10% formalin, preserved the specimens in 70% alcohol (Heyer et al. 1994), and deposited them in the Coleção Herpetológica da Universidade Federal do Amapá (voucher numbers: CECC 2200–2210, 2634–2646, 3332–3351). Euthanasia was required because specimens also had their organs analyzed as part of ongoing research on helminth parasites on anurans from the Eastern Amazon.

We included only adult specimens in the sexual dimorphism analysis. We identified sex by direct observation of the gonads, which we exposed by abdominal dissection, and by secondary sexual characteristics, such as the coloration of the vocal sac in males and the presence of oocytes in females. We measured 15 morphometric variables following Narvaes & Rodrigues (2009): snout-vent length (SVL), from tip of snout to cloacal opening; head length (HL), perpendicularly from posterior margin of tympanum to tip of snout; head width (HW), at the median portion of tympani; diameter of tympanum (DT), from posterior to anterior edges of tympanum; eye diameter (ED), from posterior to anterior corners of the eye; internarial distance (IND), between inner edge of nostrils;

interorbital distance (IOD), between inner edges of eyelids; eye-to-nostril distance (DEN), from anterior margin of eye to inner edge of nostril; snout-nostril distance (SND), from inner edge of nostril to tip of snout; arm length (AL), from axilla to the outer edge of the flexed elbow; forearm length (FAL), from outer edge of the flexed elbow to posterior edge of palmar tubercle; hand length (HAL), ventrally from posterior edge of palmar tubercle to tip of third finger; tibia length (TL), from outer edge of flexed knee to heel; thigh length (THL), from middle of cloacal opening to outer edge of flexed knee; foot length (FL), from posterior edge of metatarsal tubercle to tip of fourth toe. All measurements were taken on the right side of the body using a digital caliper (0.01 mm precision). We log₁₀-transformed all data to meet the normality requirements of statistical tests.

To reduce the effects of size on other morphometric linear measurements, we used the log version of snout-vent length (logSVL) to represent size (based on Mosimann's, 1970). The measurements for each individual were adjusted for size by taking the ratio of each variable with SVL and log₁₀-transforming the size-adjusted value:

$$\log_{10}(\text{HL}/\text{SVL}) = \log_{10}(\text{HL}) - \log_{10}(\text{SVL})$$

We applied two cluster classification analyses to discriminate morphometric variables among sexes: Principal Component Analysis and Random Forest. We conducted these analyses using SVL and all the adjusted morphometric ratios of 29 males and 14 females of *Rhinella major*. The PCA was performed using the "prcomp" function of the stats package of R software using the parameters "scale = T" and "center = T" to scale and center the morphometric variables. A Multivariate Analysis of Variance (MANOVA) was performed using the first two axes of the PCA to test whether the multidimensional morphometric space occupied differs significantly between sexes. We applied a machine learning approach based on a random forest of decision trees (Breiman 2001). Random Forest is a learning algorithm that generates classification trees from bootstrap samples of a database to aggregate results and classifies samples by choosing the best splits based on a random sample of predictors. The analysis also generates a measure of variable importance by estimating the permutation importance of each variable while leaving others unchanged on prediction error. Random Forest was conducted with 1000 trees using the "randomForest" function of the *randomForest* package in R (Liaw & Wiener 2002). Also, we performed an Analysis of Variance (ANOVA) to test for differences in Snout-Vent Length (SVL) and each of the adjusted morphometric ratios among sexes in a univariate approach.

ANOVA indicates that females were larger than males in mean SVL, head length (HL), interorbital distance (IOD), and eye-nostril distance (DEN) (Table 1). Interorbital distance (IOD), snout-vent length (SVL), foot length (FL), and Head width (HW) were the most discriminant variables between the sexes according to the PCA analysis (Table 2). The morphometric characters measured for males and females of *R. major* overlapped considerably in multidimensional space (Fig. 1a). Multivariate analysis of Variance (Manova) shows that morphometric characters of males and females are distinct for the first two axes of the PCA (Pillai trace = 0.15, degrees of freedom (df) = 2 and 40, $p < 0.04$) though Pillai's trace indicates a weak effect of sex on the variation of morphology (Pillai trace < 0.5). Our random forest classification trees showed a large overlap of characters between sexes (Fig. 1a). As expected, SVL contributed the most to the split between sexes, followed by HL and IOD (Fig. 1b). However, classification error of the confusion matrix was high, indicating that males and

females do not differ significantly in shape (Fig. 1c).

Table 1. Ranges for morphometric variables' sizes (in mm) in male and female adult *Rhinella major*. In parenthesis, mean and standard deviation. Statistics in bold are significant at alpha=0.05.

Variable	Males (n = 29)	Females (n = 14)	ANOVA
Snout-vent length	38.26–53.93 (45.19 ± 3.98)	31.45–57.14 (48.78 ± 6.42)	F=19.07 p<0.001
Head length	9.09–15.30 (12.19 ± 1.32)	11.35–16.18 (14.19 ± 1.23)	F=7.4 p=0.009
Head width	14.08–18.82 (15.84 ± 1.04)	12.26–19.68 (17.38 ± 1.76)	F=0.82 p=0.37
Tympanum diameter	1.98–3.20 (2.47 ± 0.29)	2.17–3.29 (2.59 ± 0.29)	F=0.35 p=0.55
Eye diameter	2.02–3.99 (3.01 ± 0.5)	2.31–4.93 (3.31 ± 0.72)	F=0.1 p=0.75
Internarial distance	2.23–3.89 (3.05 ± 0.35)	2.43–3.70 (3.31 ± 0.39)	F=0.017 p=0.8
Interorbital distance	3.91–7.23 (6.01 ± 0.92)	5.86–8.48 (7.29 ± 0.77)	F=5.99 p=0.01
Distance eye-nostril	3.15–5.19 (4.16 ± 0.54)	3.55–5.40 (4.87 ± 0.54)	F=3.87 p=0.05
Snout-nostril distance	1.89–2.85 (2.39 ± 0.24)	1.71–3.41 (2.61 ± 0.43)	F=0.037 p=0.8
Arm length	8.41–11.48 (10.14 ± 0.72)	7.73–12.73 (10.52 ± 1.60)	F=1.5 p=0.2
Forearm length	8.63–11.90 (10.59 ± 0.97)	7.46–12.37 (11.13 ± 1.27)	F=0.72 p=0.3
Hand length	8.21–12.10 (9.54 ± 0.85)	7.76–11.85 (10.16 ± 1.13)	F=0.084 p=0.7
Tibia length	11.33–16.93 (13.94 ± 1.23)	10.06–16.17 (14.12 ± 1.53)	F=3.68 p=0.06
Thigh length	7.90–13.53 (10.56 ± 1.22)	8.36–12.27 (11.07 ± 1.02)	F=0.362 p=0.5
Foot length	15.56–26.10 (20.95 ± 2.74)	15.05–26.19 (23.29 ± 2.93)	F=1.02 p=0.3

Table 2. Contribution of morphometric variables to the first two axes of the PCAs in multidimensional morphological spaces to explain the variation between males and females of *R. major* of Amapá state, Brazil. Bold numbers highlight the two variables with the highest contribution values for each principal component (PC). For abbreviations, see Table 1.

	PC1	PC2
SVL	-0.3575104	0.10854992
HL	0.20706481	0.38851908
HW	0.34454462	0.10797173
DT	0.21642443	-0.0710949
ED	0.23111277	0.0252638
DEN	0.25253382	0.33152874
AL	0.22145605	-0.1758608
FAL	0.25691557	-0.083706
HAL	0.26993322	-0.2845847
TL	0.27395665	-0.3618067
FL	0.12388206	0.47084835
IND	0.25501497	-0.2444581
IOD	0.23526155	0.42162558
THL	0.26823405	-0.0239712
SND	0.27555771	-0.01952
Explanation	36.5%	19.8%

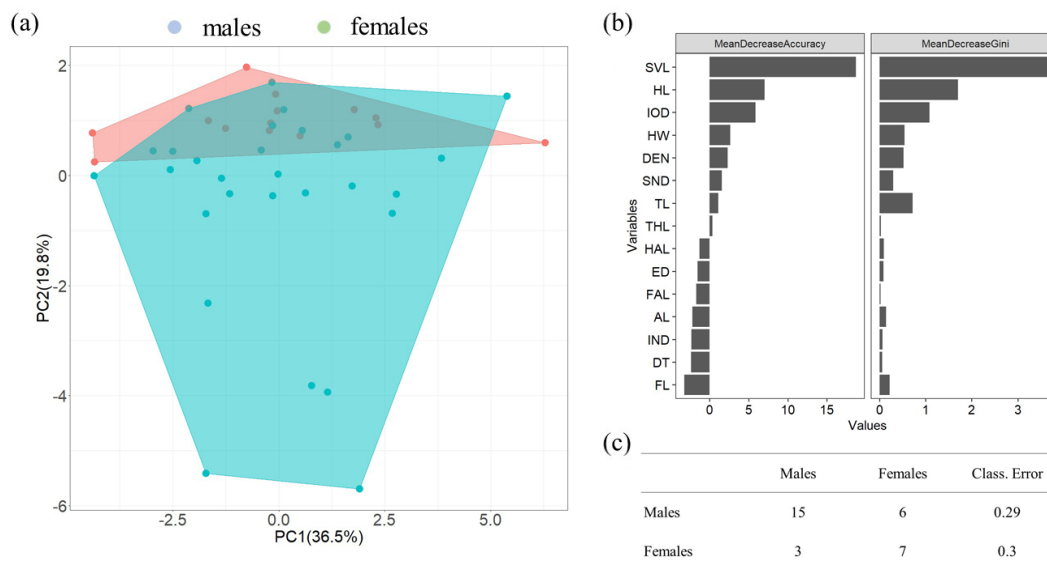


Figure 1. Results for the cluster analysis based on morphometric variables for male and female *R. major*. (a) Plot of the first and second multidimensional axis of the Principal Component Analysis. (b) Variable importance scores. (c) Confusion matrix showing the classification error of the individuals based on the analysis.

Sexual dimorphism is common in anurans, and *Rhinella major* is no exception. In the vast majority of species in this clade, females have larger body sizes (Shine 1979, Monnet & Cherry 2002). As it was found in many taxonomical anuran groups, increasing body size is likely to come with increasing benefits for females (Shine 1979, Andersson & Iwasa 1996, Green 2015). Larger females can sustain and produce more eggs per clutch (Gomez-Mestre et al. 2012, Han & Fu 2013), which can be extremely advantageous to species that lack parental care, such as *Rhinella* (Heyer et al. 1990, Haddad & Prado 2005, Stynoski et al. 2020). Reproductive effort of these species is likely to be concentrated in producing larger clutches to increase offspring survival; therefore, selection on larger females occurs (Haddad & Prado 2005, Bitar et al. 2012, Quiroga & Sanabria 2012, Pereyra et al. 2015).

One of the possible explanations for a larger male size in anurans is territorial behavior; larger males can defend territories and attack other males more successfully (Shine 1979, Shuster & Wade 2003). However, as territorial behavior or aggressive interactions were never observed in *Rhinella major*, the larger size is not a clear reproductive advantage in the male sex. This is a possible reason why the increase in female body size is not followed by a comparable increase in male body size in most species of anurans (Crump 1996, Brown et al. 2010).

Besides sexual selection, some ecological pressures related to life-history traits, such as growth or age at maturity, sustain alternative hypotheses to explain sexual size dimorphism (Arantes et al. 2015, Otero et al. 2017). For example, studies demonstrated that a decrease in male size might be due to a higher male mortality rate, resulting in earlier male maturation compared to females (Trivers 1974, Monnet & Cherry 2002). As well as sexual dimorphism can arise during the embryonic phase due to sex differences in

growth. Variation in growth between sexes during developmental stages implies different susceptibilities to similar ecological conditions (Richner 1991). For instance, the body size of anurans may be a trait associated with resource acquisition, and morphological differences may be associated with food niche partitioning between sexes (Hedrick & Temeles 1989, Herrel et al. 1999), also observed in some snakes (Camilleri & Shine 1990, Vincent et al. 2004), lizards (Cooper & Vitt 1989, Vincent & Herrel 2007, Taverne et al. 2019), turtles (Bulté et al. 2008) and anurans (Quiroga et al. 2015, Magalhães et al. 2016, Hudson et al. 2018).

Our quantitative analysis adds further evidence of female-biased SSD in anurans and represents the first description of sexual dimorphism in *R. major*. On this matter, a number of specific hypotheses have been addressed to explain female-biased sexual size dimorphism in the vast majority of anuran species (Shine 1979). However, to investigate the causes of sexual size dimorphism, tests of several hypotheses are required and must be integrative (Blanckenhorn 2005). Case studies of particular species allow direct comparisons and integration of information on intraspecific morphological variation and improve the database available for subsequent analysis to evaluate general patterns of sexual dimorphism in anurans from Amazon. To extend between-population analyses, it would be insightful to compare this study with patterns found in other populations of *R. major* from both urban and natural landscapes.

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