Trabajo

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Sexual size dimorphism in selected traits of *Leptodactylus luctator* (Anura: Leptodactylidae)

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ABSTRACT
Sexual dimorphism reveals a broad variation in morphological, physiological, and behavioral traits related to organismal life strategies. Anurans are particularly suitable for studying the origin, integration, and diversification of sexual dimorphism, owing to the high degree of variation observed in size and secondary sexual characteristics, as well as the diversity of life histories and their complex biphasic cycle. In this study, a morphometric characterization of *Leptodactylus luctator* is conducted to investigate whether sexual dimorphism is present. A total of 18 variables were measured in the head, body, and limbs of males and females from a population located in wetlands near Ucacha town, Córdoba Province, Argentina. *Leptodactylus luctator* exhibited more robust limbs in males, but longer fingers in females. Furthermore, females showed a greater axilla-groin length, indicating differences in body shape between sexes in addition to size. Given that larger forelimbs in males have been associated, in the literature, with greater reproductive success, while finger length has been correlated with different levels of circulating sex hormones, the possible selection pressures related to the observed variation are discussed herein.

Key words: Sexual differences; Wrestler Frog; Digit length; Robust limbs.

Introduction

In anuran species, males and females often exhibit various characteristics differences, including body size and shape, coloration, sex-specific structures, and physiological and behavioral traits (Shine, 1979, Halliday and Verrell, 1986; Kupfer, 2007). Sexual selection drives the development of secondary sexual characteristics, such as vibrant colors, larger limbs, fangs, or spines, while natural selection mitigates intersexual competition through ecological adaptations such as niche segregation, predator-prey interactions, or ontogenetic differences (Fairbairn *et al.*, 2007, Bell and Zamudio, 2012).

The analysis of evolutionary patterns influencing sexual dimorphism in anurans and its ecological implications has predominantly centered on adult body size (Shine, 1979; Halliday and Verrell, 1988; Monnet and Cherry, 2002; Portik *et al.*, 2020). In approximately 90% of anuran species, females are larger than males (Shine, 1979). While this size dimorphism has been attributed to increased fecundity in larger females (Woolbright ,1983), alternative proximate causes, including sexual differences in growth rate, age structure, age at sexual maturity, adult survival, or microhabitat use, have been proposed (Halliday and Tejedo, 1995; Monnet and Cherry, 2002; Hasumi, 2010; Silva *et al.*, 2020). Moreover, in species with male combat, selection favors larger males due to success in intrasexual struggles (Shine, 1979; Wells and Schwartz, 2007). Despite females being substantially larger in body size, males often surpass them in other body dimensions such as head size, limb morphology, and others (see Lee, 2001).

Previous studies evaluating sexual divergence in the genus *Leptodactylus*, particularly those focusing

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on head dimensions, nasal region morphology, and nest-digging behavior, revealed an absence of sexual dimorphism (Ponssa and Barrionuevo, 2012; Ponssa and Medina, 2016; Camurugi *et al.*, 2017; Marangoni *et al.*, 2019). The unique difference observed was the sharper snout of males, associated by the authors with natural selection for constructing a more optimal incubation chamber (Ponssa and Barrionuevo, 2012; Ponssa and Medina, 2016). Other studies indicated the absence of sexual size dimorphism in larger-sized species, allowing smaller males to reproduce, thus weakening selection for larger males (Laufer *et al.*, 2014). Instead, favoring other traits crucial in male competition, amplexus maintenance, or parental care, such as hypertrophied forearm muscles, large testes, or the presence of spines in males, or longer tibia in females related to parental care behavior (Camurugi *et al.*, 2017).

Among leptodactylids, *Leptodactylus luctator* exhibits an unusual pattern of SSD where males are larger than females, a rarity among anuran species, accounting for only 7.5% of known species (Pincheira-Donoso *et al.*, 2021). During axillary amplexus, males of *L. luctator* secure females with robust forelimbs and keratinized thumb spines, providing a better grip while releasing glandular secretions, resulting in a foamy mass where eggs develop (Rodrigues *et al.*, 2011). Females protect tadpoles until metamorphosis, though males may protect them as well (reviewed by Carrillo *et al.*, 2023). Despite no differences in age at sexual maturity or longevity between sexes, there are diet variations (Maneyro *et al.*, 2004; Pazinato *et al.*, 2011; López *et al.*, 2017). Recent research by Goldberg *et al.* (2024) found no sexual dimorphism in 10 morphometric traits in *L. luctator*, except for snout-vent length. This unique SSD pattern in *L. luctator* underscores the complexity of sexual selection and the diverse evolutionary pressures acting on different species.

Given the striking characteristics of *Leptodactylus luctator* and its specific behaviors such as signals for combat potential, the need for physical anchoring due to large adult size (Camurugi *et al.*, 2017), or maternal care (Rodrigues *et al.*, 2011; Carrillo *et al.*, 2023), we attempt to explore the possibility of other potentially dimorphic measures in this species that have not been considered elsewhere. Recently, new dimorphic traits have been included to expand our understanding of intersexual differences and their evolution in anurans. Thus, to better comprehend the core of sexual dimorphism, it's crucial to delve into new research areas, investigating the presence of other dimorphic traits that have not received enough attention due to a predominant emphasis on absolute size differences between males and females.

Our focus centers, particularly but not exclusively, on limb characteristics that are usually overlooked and are linked to these behaviors. For example, dissimilarities in the selective pressures associated with structurally distinct microhabitats may give rise to morphological variations in anatomical structures implicated in locomotion (Navas and James, 2007; Herrel *et al.*, 2012; Petrović *et al.*, 2017). However, it is crucial to recognize that such variations may not solely be a consequence of selection acting on locomotor traits; rather, they could also be an outcome of selection operating on other morphological aspects, such as the 2D:4D digit ratio, a feature that serves as a potential illustrative paradigm for these hypothetical scenarios (Gomes and Kohlsdorf; 2011; Lofeu *et al.*, 2017). This specific trait is implicated in locomotor functions and, therefore, might exhibit divergence in response to ecological differentiation observed among distinct lineages. Nevertheless, it is equally plausible that alterations in digit proportions occur exclusively as a repercussion of modifications in developmental programs triggered by a differentiated sensitivity of specific digits to sex steroids during development (Gomes and Kohlsdorf; 2011; Lofeu *et al.*, 2017). While traditional assessments have primarily focused on body size dimorphism, our exploration extends to overlooked limb and head characteristics associated with specific behaviors in *L. luctator*, shedding light on potential dimensions of sexual selection that have yet to be considered.

Material y methods

Morphological data were obtained from mature individuals (20 females; 50 males), collected in monthly samplings from wetlands near the town of Ucacha (33° 01`S; 63° 30`W; 193 m.a.s.l.) in the Province of Córdoba, Argentina. To ensure the breeding maturity and condition of all individuals, we collected specimens exclusively on chorusing nights at reproductive sites. Sex and identification of mature specimens were determined by visual inspection of secondary sexual characters in males, and the presence of ovarian follicles in females. In the laboratory, they were sacrificed by concentrated benzocaine. The animal care and use protocols have been reviewed and approved by the Comité Institucional para el Cuidado y Uso de Animales de Laboratorio (CICUAL), Instituto de Diversidad y Ecología Animal (IDEA-UNC-CONICET). Specimens are stored at the herpetological collection of the Museo de Zoología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba (Argentina) with the numbers AC711 to AC781. We measured (Fig. 1): snout–vent length (SVL), internasal distance (ND), snout length (SL), head length (HL), thigh diameter (TD), biceps diameter (BD), forearm diameter (FD), lower leg diameter (LD), axilla-groin length (AGL), and fingers (FII-FV) and toes (TI-TV) lengths following Mendez and Correa-Solis (2009), Watters et al. (2016) and Lofeu *et al.* (2017). Measurements were taken by the same person (J. Salguero) with a digital caliper (precision 0.01 mm). All characters measured were tested for normality (using a modified Shapiro-Wilks test) and homogeneity, and transformed using a log transformation. An analysis of covariance (ANCOVA) was used to assess sexual dimorphism adjusted to body size using SVL as the covariate. We included the interaction SVL * sex, which we retained in the model when significant and omitted when non-significant. A t-test was also carried out to evaluate the direction of dimorphism. To assess sexual size dimorphism (SSD) for each trait, we utilized the sexual size dimorphism index (SDI) as described by Lovich and Gibbons (1992). This index was computed by dividing the mean trait length of females by the mean trait length of males and then subtracting 1. The resulting value offers an approximate estimation of the magnitude of sexual size dimorphism. Positive values indicate a bias towards larger females, reflecting female-biased dimorphism, while negative values indicate the opposite pattern.

Results

Figure 2 illustrates the variability of the size dimorphism index for each trait, with some traits showing a more male or female bias. The values, although low, were negative for BD and FD indicating a bias to be larger in males whereas all the other measurements were female-biased.

When the data were adjusted for body size using ANCOVA, some of the previous results were supported, while others were rejected (Table 1). In all cases, the ANCOVA model retained the SVL variable because of its significance, which indicates that size-corrected analyses are crucial.

The ANCOVA results, which account for the effect of SVL, revealed that of the 17 morphological variables measured, four showed differences between sexes (Table 1).

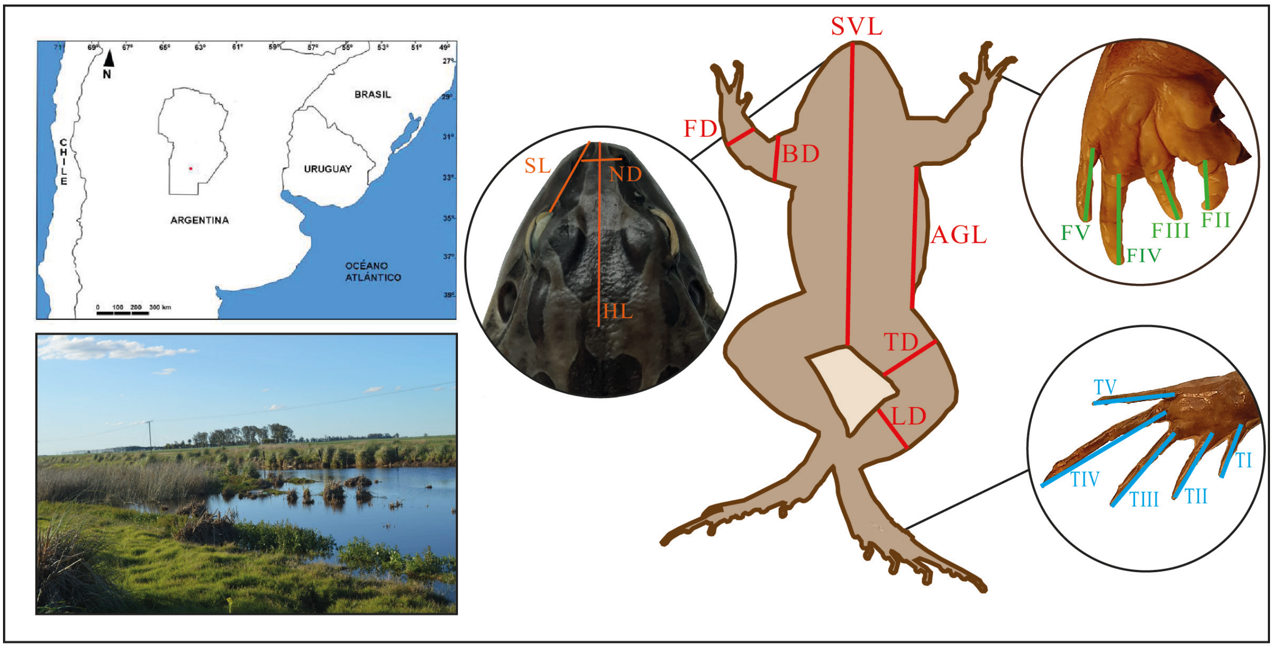

Figure 1. At left, map of the site location where specimens of *Leptodactylus luctator* were sampled with a representative photograph of the environment inhabited by the species. At right, the 18 morphological attributes measured. Abbreviations: snout–vent length (SVL), internasal distance (ND), snout length (SL), head length (HL), thigh diameter (TD), biceps diameter (BD), forearm diameter (FD), lower leg diameter (LD), axilla-groin length (AGL), and fingers II to V (FII-FV) and toes I to V (TI-TV).

Males had thicker biceps (BD) and forearms (FD) but a shorter Finger II (FII) and a shorter distance between limbs (AGL) than females (Fig. 3). We also found no differences between sexes in digit ratio.

Discussion

The Wrestler Frog, *Leptodactylus luctator*, exhibits noticeable sexual dimorphism in the snout-vent length (SVL) of mature adults, with males being larger (Goldberg *et al.*, 2024). However, most previously examined physical characteristics, including 2D:4D ratios, have demonstrated monomorphism in this species. Recent findings by Goldberg *et al.* (2024) revealed that out of 10 measured traits, only SVL displays sexual dimorphism, indicating that the addition of 17 new variables results in only 5 out of 27 traits appearing dimorphic in this species. Most studies identified sexual selection as the primary driver propelling males towards larger bodies, providing them with a competitive advantage in resource acquisition, such as food and space, ultimately enhancing reproductive success (De Lisle, 2019).

The most pivotal variable distinguishing between sexes is the forelimb diameter, playing a crucial role during amplexus and male reproductive success. Previous studies have primarily explored intersexual differences in frog limb muscles through muscle mass examinations or muscle fiber types and sizes (Lee, 2001; Lee and Corrales, 2002; Clark and Peters, 2006; Navas and James, 2007; Li *et al.*, 2023). Forelimb diameter, essential for maintaining a grip during amplexus, is associated with male reproductive success. Larger limb muscles and fiber sizes empower males to resist takeovers by competing males during amplexus. The prevalence of amplexus in frogs has led to the evolution of sexual dimorphism in forelimb muscles, with certain muscles (i.e., such

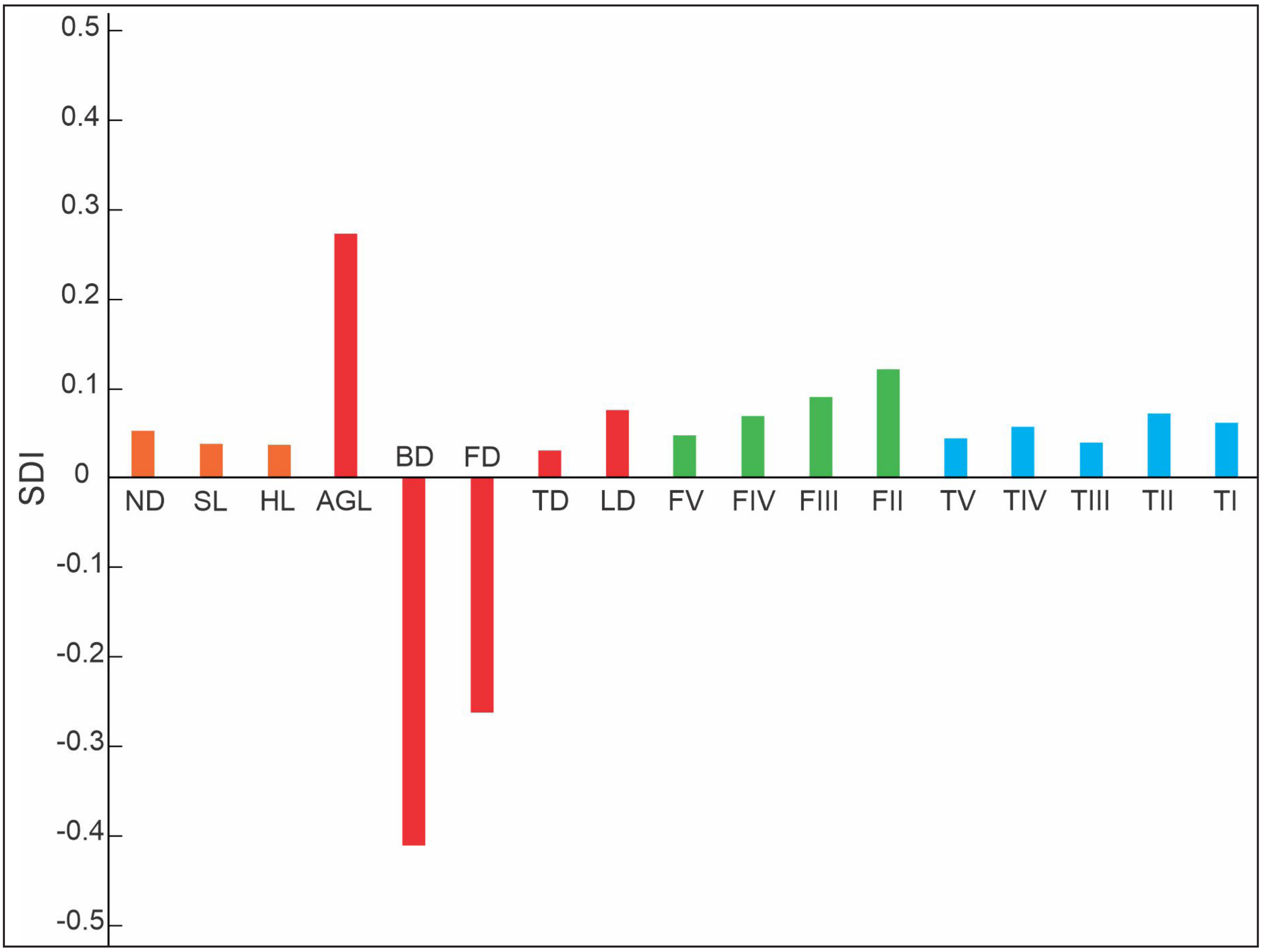

Figure 2. Size dimorphism index (SDI) across 17 measured traits (not adjusted to SVL) in *Leptodactylus luctator*. Positive values indicate female-biased dimorphism whereas negative values indicate male-biased dimorphism. Abbreviations: snout–vent length (SVL), internasal distance (ND), snout length (SL), head length (HL), thigh diameter (TD), biceps diameter (BD), forearm diameter (FD), lower leg diameter (LD), axilla-groin length (AGL), and fingers (FII-FV) and toes (TI-TV). The colors of the bars follow Figure 1.

Table 1. Results from the ANCOVA analysis for the traits comparisons (SVL as a scaling factor) between males and females of *Leptodactylus luctator*. The F and P-values (significant values for sexual dimorphism are in bold) for each comparison are represented. An indication of the sex that displays larger size (F, for females, M, for males, and ns, for non-significant differences) is also given.

Variable	F	p	Larger sex
ND	0.60	0.4417	ns
SL	0.02	0.9003	ns
HL	0.01	0.9234	ns
TD	0.42	0.5198	ns
BD	**30.18**	**<0.0001**	**M**
FD	**28.03**	**<0.0001**	**M**
LD	0.41	0.5247	ns
AGL	**21.92**	**<0.0001**	**F**
FII	**4.81**	**0.0325**	**F**
FIII	2.64	0.1094	ns
FIV	3.47	0.0675	ns
FV	0.18	0.6716	ns
TI	0.51	0.4788	ns
TII	2.08	0.1550	ns
TIII	0.10	0.7518	ns
TIV	0.86	0.3563	ns
TV	0.27	0.6083	ns
FII:FIV	2.81	0.0990	ns
TII:TIV	0.63	0.4311	ns

as *pectoralis, coracoradialis, coracobrachialis, flexor carpi radialis, extensor carpi radialis, sternoradialis*, and *abductor indicus longus*) being larger in mass in males than females. Larger male forearm diameter is linked to higher reproductive success through agonistic interactions, access to larger females, and increased population densities (Halliday and Verrell, 1986; Kupfer, 2007; Liao *et al.*, 2013). It appears that robust forelimbs and thumb spines are not evolved as signals for combat potential but rather as a physical necessity for anchoring to females due to their large adult size (Duellman and Trueb, 1986; Heyer, 2005).

In a large survey of 146 species, Juarez *et al.* (2023) showed that females have leg muscles with 42% more volume than those of males after accounting for differences in body length. Contrarily, we found no sexual differences in hind limb muscles. Goldberg *et al.* (2024) found no sexual differences in other traits such as arm length or tibia length, challenging the expected dimorphism in *L. luctator* due to robust forelimb muscles in males and specific behaviors in females in which a longer tibia may enhance female success in defending the shoal (stronger propulsion to combat predators or for digging channels faster), respectively (Rodrigues *et al.*, 2011; Carrillo *et al.*, 2023).

Even when sexual size dimorphism in SVL is male-biased, certain female features are larger. Notably, the space between the axilla and groin relative to the snout–vent length of female adults is significantly greater than that of males. This larger space likely accommodates a larger abdominal volume to support larger ovaries and increased ovum production, thereby enhancing fertility and reproductive capacity. Consequently, sexual dimorphism in trunk length, indicating the distance between limbs in this study, correlates with a fecundity advantage.

Our study unveils a lack of consistent sexual differences in 2D:4D in the fore and hind limbs of *L. luctator*. The second-to-fourth digit ratio (2D:4D) is known for its sexual dimorphism in humans and other vertebrates and is hypothesized to arise based on the influence of maternally derived prenatal androgens on the genes Hox (Voracek, 2011). The study of 2D:4D is important because it is a potential indicator of an individual's prenatal hormone environment and past developmental pathways. Among anurans, although no intensive study has been carried out, results are controversial. Some species exhibited a larger digit ratio in males whereas there were no sex differences in others, varying between fore and hind limbs (Chang, 2008, Germano *et al.*, 2011; Direnzo and Stynoski, 2012; Beaty *et al.*, 2016; Lofeu *et al.*, 2017). Despite finding no significant differences between sexes in *L. luctator*, females tend to present larger ratios than males.

A concern about the identity of Finger II arises because depending on the theoretical framework, some authors might consider that the four fingers represent Finger I to IV whereas others, including us, consider that Finger I is lost in the manus based on a developmental pathway after Fabrezi *et al.* (2017). In such a context, comparisons of digit ratio patterns across different species may pose challenges because what most authors are comparing are fingers III and V. This implies a problem of homology between fingers and toes (Fabrezi *et al.*, 2017). Nevertheless, the finger ratio IIID:VD also showed no sexual differences (p = 0.11) in *L. luctator*. Conversely, we observed differences only in the length of Finger II, with females exhibiting larger dimensions.

Lofeu *et al.* (2017) described that in *Leptodac-*

tyls podicipinus and *L. fuscus*, male-biased 2D:4D digit ratios originated from a differential sensibility of digit II developing tissues to circulating testosterone and explained that sensitivity in one specific digit could evolve through changes in steroid receptors concentrations in specific phalanges of that digit. While the functional significance of this dimorphism remains unclear, it may not be a direct target of selection but rather an indirect response to variable exposure to androgens during early development. Multiple-trait effects of hormonal variation are especially evident in sexually dimorphic phenotypes. A wide body of literature demonstrated the androgenic basis of sexually dimorphic limb muscles, color, body shape, and digit lengths (e.g., Emerson, 2000; Sever and Staub, 2011; Kampe and Peters, 2013; Lofeu *et al.*, 2017), adding new traits in the search of dimorphic traits that provide an additional perspective for interpreting patterns of sexual dimorphism.

Finally, a concern arises regarding the extent of sexual dimorphism within a single population, particularly when considering the geographical variations in sexual size dimorphism (SSD) documented in other species (Schäuble *et al.*, 2004; Yu *et al.*, 2010; Goldberg *et al.*, 2018). These authors have identified various climate gradients, as well as latitude and longitude, as significant factors influencing SSD variation. Given that widespread species offer suitable models for assessing this phenomenon due to the distribution of their populations across diverse geographical and climatic gradients, *Leptodactylus luctator* emerges as a compelling alternative model. The limited presence of distinct dimorphic traits in this species presents an opportunity to delve into the complex interplay between morphology and several pivotal environmental and evolutionary factors that may influence morphological variation.

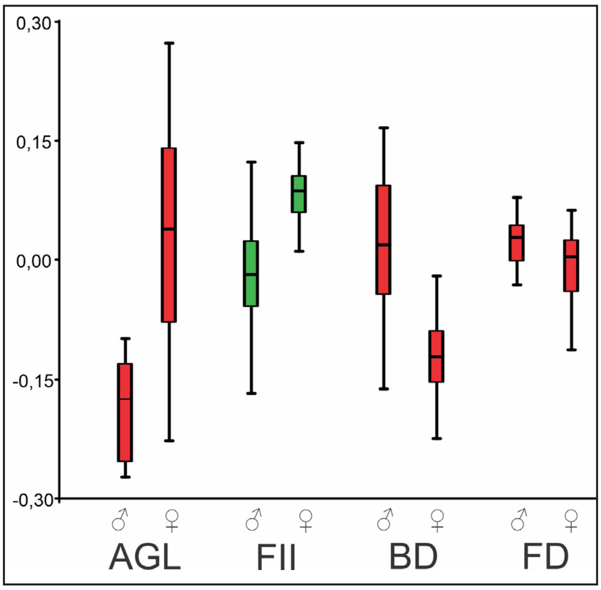

Figure 3. Sexual dimorphism in *Leptodactylus luctator*. Boxplots showing residuals extracted from linear models between the target variable and covariable to exclude the effect of size. All variables were previously log-transformed. The lines are medians; the boxes and whiskers are the quantiles. Abbreviations: axilla-groin length (AGL); finger II (FII); biceps diameter (BD), forearm diameter (FD). The colors of the bars follow Figure 1.

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