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Allometric patterns in *Potamotrygon motoro* (Myliobatiformes: Potamotrygonidae): insights into sexual and ontogenetic variation

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Potamotrygon is the most species-rich genus of Neotropical freshwater stingrays in the Potamotrygoninae, currently comprising 31 species primarily diagnosed by coloration patterns, dermal denticles, and body measurements. Although morphometric characters are fundamental for species descriptions, their growth patterns can vary throughout an individual's life, especially due to sexual dimorphism and ontogenetic changes. However, these aspects have not been investigated in detail in potamotrygonins. This study aims to explore allometric growth patterns in *Potamotrygon motoro*, examining ontogenetic and sexual allometry across 25 body measurements. Our results reveal that pelvic fin width and the interocular distance exhibit distinct allometric patterns between males and females. Considering developmental stages, clasper structures in males grow 1.85 to 2.99 times faster in juveniles than in adults. Understanding these allometric patterns is particularly significant for *P. motoro*, and can aid in species identification and delimitation, given its broad distribution and notable polychromatism.

Keywords: Growth patterns, Morphometric analysis, Neotropical freshwater stingrays, Sexual dimorphism, Standardized Major Axis analysis.

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Potamotrygon é o gênero mais rico em espécies das raias Neotropicais de água doce em Potamotrygoninae, atualmente compreendendo 31 espécies diagnosticadas principalmente por padrões de coloração, dentículos dérmicos e medidas corporais. Embora os caracteres morfométricos sejam fundamentais para a descrição de espécies, seus padrões de crescimento podem variar ao longo da vida de um indivíduo, especialmente devido ao dimorfismo sexual e mudanças ontogenéticas. No entanto, esses aspectos não foram investigados em detalhes nos potamotrigoníneos. Este estudo tem como objetivo explorar os padrões de crescimento alométrico em *Potamotrygon motoro*, examinando a alometria ontogenética e sexual em 25 medidas corporais. Nossos resultados revelam que a largura das nadadeiras pélvicas e a distância interocular apresentam padrões alométricos distintos entre machos e fêmeas. Considerando os estágios de desenvolvimento, as estruturas do clásper crescem entre 1,85 a 2,99 vezes mais rapidamente nos juvenis que nos adultos. Compreender esses padrões alométricos é particularmente relevante para *P. motoro*, podendo auxiliar na identificação e delimitação da espécie, considerando sua ampla distribuição e polimorfismo de coloração.

Palavras-chave: Análise de Eixo Maior Padronizado, Análise morfométrica, Dimorfismo sexual, Padrões de crescimento, Raias de água doce neotropicais.

INTRODUCTION

The genus *Potamotrygon* currently encompasses 31 valid species (Fricke *et al*., 2026) of stingrays with short, thick tails bearing a pointed spine at their posterior portion (Loboda, 2010; Lasso *et al*., 2013; Carvalho, 2016). Among these, *Potamotrygon motoro* (Müller & Henle, 1841) has the broadest distribution within the genus, occurring in the three largest South American river basins: the Amazon, Paraná-Paraguay, and Orinoco (Rosa, 1985; Compagno, Cook, 1995; Carvalho *et al*., 2003). However, diagnosing *P. motoro* is challenging due to its extensive distribution and pronounced polychromatism (Rosa, 1985; Loboda, Carvalho, 2013). Recent taxonomic revisions have revealed that part of what was previously identified as *P. motoro* actually represents newly described species, distinguished by specific color patterns and with more restricted distributions (*e.g*., *Potamotrygon amandae* Loboda & Carvalho, 2013; *P. marquesi* Silva & Loboda, 2019). Despite these advancements, morphometric measurements (Rosa, 1985; Loboda, 2010; Rincon *et al*., 2019), along with coloration patterns, remain as the primary diagnostic characters for distinguishing *P. motoro* from its congeners (*e.g*., *P. leopoldi* Castex & Castello, 1970; *P. rex* Carvalho, 2016).

Morphometric data are extensively used in the delimitation and description of *Potamotrygon* species (*e.g*., Fontenelle *et al*., 2014, 2017; Carvalho, 2016). However, it is expected that some morphometric characters may exhibit variations in growth patterns throughout an individual's life or between sexes (Loboda, 2010). Despite that, growth pattern variation has rarely been addressed in detail in *Potamotrygon* taxonomy, with only superficial or anecdotal mentions in the literature (*e.g*., Loboda, Carvalho, 2013; Rincon *et al*., 2019) or analyses limited to a few structures (Moreira *et al*., 2018). Typically,

species descriptions do not account for potential sexual dimorphism or ontogenetic changes in morphometric data (*e.g.*, Carvalho *et al*., 2011; Silva, Carvalho, 2011a): even when such data are used for species diagnosis, sexual or ontogenetic changes are barely treated (*e.g.*, Silva, Carvalho, 2011b; Fontenelle *et al*., 2014; Fontenelle, Carvalho, 2017). Given that *Potamotrygon motoro* represents one of the most notable most notable species of the genus, understanding its growth patterns can not only aid in its accurate diagnosis but also contribute to refining the taxonomy of the genus as a whole.

Growth patterns can be analyzed statistically by applying models that evaluate variation in size, allowing correlations with sex and developmental stages to be established. One effective way to study growth patterns statistically is through allometry, which examines the relationship between the size of a particular body part and the overall size of the organism (Whitlock, Schluter, 2015). In biology, allometry is widely used to identify patterns of differential growth, enabling researchers to assess how body proportions change with development and to correlate these changes with factors such as sex and developmental stages (Whitlock, Schluter, 2015). This approach is particularly valuable in identifying growth trajectories and understanding morphological variation within and between species across several animal groups (*e.g.*, Alberch *et al*., 1979; Cheverud *et al*., 1983; Atchley, 1984; Smith *et al*., 1985; Klingenberg, Zimmermann, 1992; De-Lima *et al*., 2019; Citeli *et al*., 2022).

Ontogenetic, static, and evolutionary allometries are recognized depending on whether the relationship is examined over the development of an individual, across individuals at a similar developmental stage within a population, or across separate evolutionary lineages (Cock, 1966; Gould, 1966; Cheverud *et al*., 1983; Klingenberg, 1998; Voje, Hansen, 2014). Static allometry refers to patterns of variation and covariation of traits among individuals within a specific ontogenetic stage (Gould, 1966: individual allomorphosis). Ontogenetic allometry focuses on the covariation of traits across different ontogenetic stages (Gould, 1966). Evolutionary allometry examines the covariation of traits among organisms from various evolutionary lineages that share a common ancestor and are in a single ontogenetic stage (Gould, 1966: interspecific allometry).

Morphological traits are usually strongly correlated with body size, often following a linear regression of $Y = a + bX$, where Y is the response variable to the explanatory (fixed) variable X; the coefficient b is the slope of the line, indicating the degree of inclination relative to the x-axis; and the coefficient a is the Y-intercept (the value of Y when X is zero). Based on the value of the slope, the allometric pattern is classified into three types. Positive allometry occurs when the variable Y grows at a rate higher than the growth rate of the X variable (proxy), resulting in a slope $b > 1$. Negative allometry happens when the variable Y grows at a slower rate than the X variable, leading to a slope $b < 1$. Isometry occurs when the variable Y grows at the same rate as the X variable, with a slope $b = 1$ (Jolicoeur, 1963; Shingleton, 2010). In this case, growth is proportional. Thus, analyzing the slope allows us to classify and understand the different patterns of allometric growth in the studied variables (Shingleton, 2010).

Many allometry studies emphasize the relative stability of the allometric coefficient, used to describe the correlation between the growth of different parts of an organism, compared to the intercept (Huxley, 1924; Huxley, Teissier, 1936; Cock, 1966; Gould, 1971; Klingenberg, 1998; Voje, Hansen, 2014). Consequently, the prevailing hypothesis suggests that allometry constrains long-term evolutionary change, evolving slowly and

resulting in a certain conservatism in form (Gould, 1966; Gould, 1971, but see the difference between Huxley-Jolicoeur and Gould-Mosimann approaches to allometric studies in Klingenberg, 1998, 2016). Therefore, understanding allometric patterns is valuable to taxonomy and systematics, providing insights into the morphological evolution of a group over time. This study provides the first description of ontogenetic and sexual allometric patterns in a Neotropical freshwater stingray, based on morphometric analyses of multiple body structures, and discusses how these patterns may relate to those of its congeners.

MATERIAL AND METHODS

Material. A total of 91 individuals of *Potamotrygon motoro* (Fig. 1) were examined, from the respective collections: Centro de Investigaciones Antropológicas, Arqueológicas, Paleontológicas and Colección Zoológica (CZUT-IC); Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva (IAvH); Instituto de Ciencias Naturales, Bogotá (ICN - UNAL); Instituto de Investigaciones de la Amazonia Peruana, Iquitos (IIAP); Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA); Museum für Naturkunde, Berlin, Germany (ZMB); Muséum national d'Histoire naturelle, Paris (MNHN); Museu de Historia Natural, Lima (MUSM); Naturhistorisches Museum, Vienna (NMW); Zoologisches Museum der Humboldt-Universität (ZMH). Specimens were identified according to Loboda (2010). Also, specimens recently collected by the IAvH during the second author's visit to the institution were examined and referred to here as uncatalogued ("uncat.").

The specimens were pre-categorized according to their developmental stage (DS) into juvenile or adult. These categories were defined based on morphological aspects that change during development, such as the rigidity and size of the clasper in males, and tooth development and body size in females (Loboda, 2010). They were also categorized by sex based on the presence of claspers in males. All individuals were measured according to the protocols of Bigelow, Schroeder (1953), Rosa (1985), and Taniuchi, Ishihara (1990), for a total of 25 measurements (Tab. 1), taken with a digital caliper with an accuracy of 0.01 mm or a measuring tape with an accuracy of 1 mm (raw data are provided in Tabs. **S1**, **S2**). Two measurements are related to clasper and were only taken in males. All supplementary files, datasets and scripts are available at https://doi.org/10.6084/m9.figshare.30251551.

Statistical analysis. All measurements were log-transformed and visual inspection of residuals did not indicate strong deviations from normality or heteroscedasticity. Disc width (DW) was used as a proxy for body size (Wagiyo *et al.*, 2023), and ontogenetic and sexual allometry were investigated. The allometric coefficients (b) were estimated as the slope of linear regressions of trait values against DW, and allometric patterns were classified according to their traits and directions (*i.e.*, isometry, if $b=1$; positive, if $b>1$; or negative allometry, if $b<1$). Subsequently, a Standardized Major Axis analysis (SMA) was used to test whether there is a difference in the allometric coefficient (b) (1) throughout ontogeny (between juveniles and adults) and (2) regarding sex (between males and females, for all measures except those involving claspers). Clasper measurements were

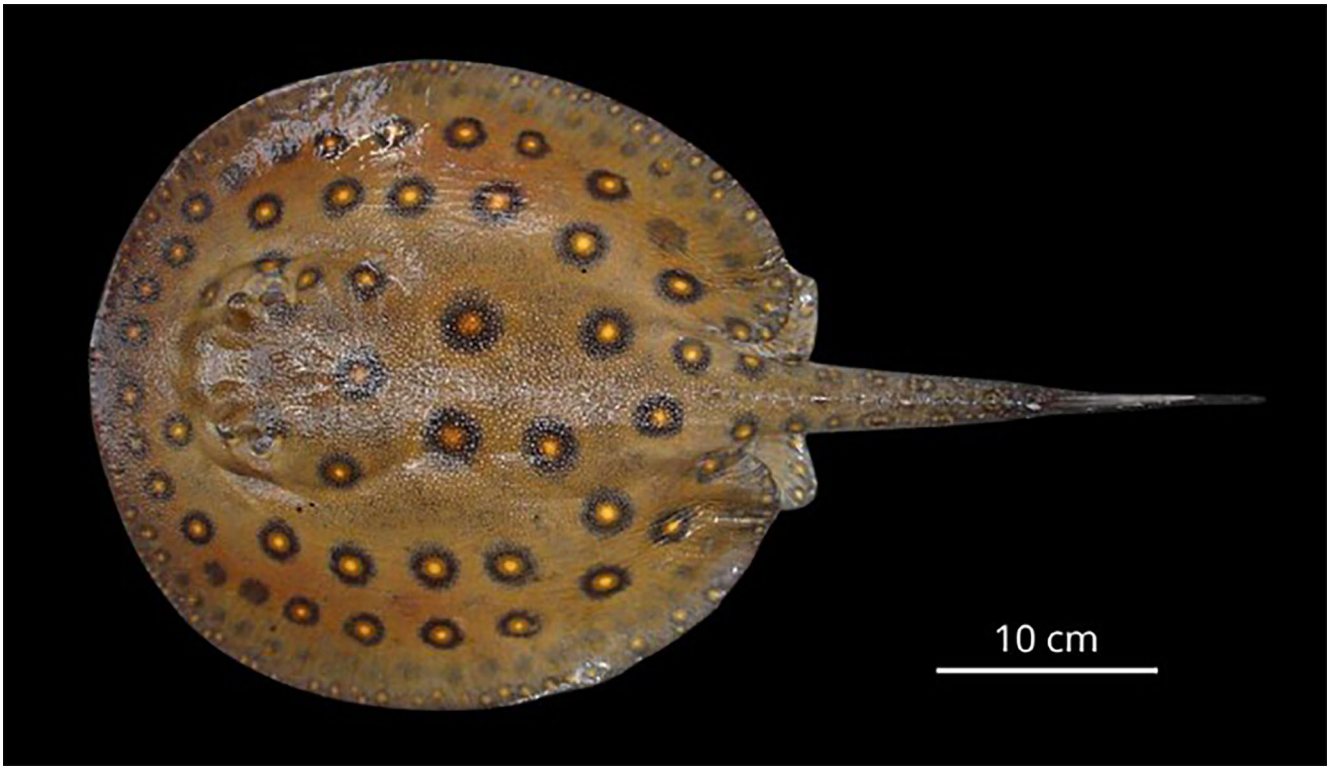

FIGURE 1 | *Potamotrygon motoro*, adult female, MZUSP 104288, 539 mm CT. Photo by Fernando Marques.

TABLE 1 | Morphometric data analyzed in this work and their abbreviations.

Measurements	Abbreviations
Disc Width	DW
Tail Length	TL
Tail Width	TW
Interspiracular Distance	IED
Interocular Distance	IOD
Eye Length	EL
Spiracle Length	SL
Preorbital Length	POrbitalL
Prenasal Length	PNasalL
Precloacal Length	PCloacalL
Preoral Lenght	POralL
Internasal Distance	IND
Mouth Width	MW
Distance between the 1st pair of gill slits	D1stG
Distance between the 5th pair of gill slits	D5thG
Branchial Basket Length	BBL
Pelvic Fin Length	PFL
Pelvic Fin Width	PFW
Clasper External Length	CEL
Clasper Internal Length	CIL
Sting Length	SL
Axilla of the Pelvic Fin	APF

compared between juveniles and adults of male specimens. To account for multiple comparisons, table-wide *p*-values obtained from SMA tests were adjusted using the Bonferroni correction (Rice, 1989). The interpretation of the results considered both the statistical significance (α) and the quality of model adjustment (determination coefficient, r^2), to balance both type-I and type-II errors (Chandler, 1995). The significance level adopted for this work was $p < 0.05$ after adjustment, but differences with *p*-value < 0.1 (after Bonferroni correction) associated to $r^2 > 0.80$ were also considered biologically relevant and are presented in the results. All analyses were performed in the R software v. 4.0.2 (R Development Core Team, 2023), using RStudio (RStudio Team, 2016) and the packages *car* (Fox, Weisberg, 2019), *dplyr* (Wickham *et al*., 2023), *ggplot2* (Wickham *et al*., 2024a), *progress* (Csárdi, FitzJohn, 2023), *purrr* (Wickham, Henry, 2023), *readxl* (Wickham, Bryan, 2023), *smatr* (Warton *et al*., 2012), *stringr* (Wickham, 2023); *tibble* (Müller, Wickham, 2023) and *tidyr* (Wickham *et al*., 2024b).

RESULTS

Our dataset presents 31 female and 60 male specimens, categorized as 42 adults and 49 juveniles. Overall, all head and tail measurements were strongly correlated with Disc width. Of the measurements analyzed, two showed significant differences in growth rates between sexes at $p < 0.05$ (and one more at $p < 0.1$) after the Bonferroni correction; and the two clasper measurements differed between juvenile and adult males (Tabs. 2, 3, **S3**, **S4**; Fig. 2).

Males and females exhibited distinct growth patterns in the pelvic-fin width, interocular distance and, if we adopt a 10% type I error rate, in the distance between the first pair of gill slits (Tab. 2). The pelvic fin width demonstrated significant sexual dimorphism ($p = 0.000$), with females exhibiting a more positive slope ($b = 1.276$) than males ($b = 0.997$, isometry), meaning this structure grows 1.28 times faster in females relative to DW. The interocular distance showed near-isometric growth in males ($b = 0.966$) but positive allometry in females ($b = 1.130$), indicating that this structure grows approximately 1.17 times faster in females relative to DW. The distance between the 1st pair of gill slits, despite displaying positive allometry in both sexes, females had a higher slope ($b = 1.167$) compared to males ($b = 1.061$), meaning this distance grows 1.10 times faster in females relative to DW.

TABLE 2 | Summary of the statistics for regressions of body traits *vs*. disc width (DW), comparing the sexes. n- number of analyzed specimens, *b*- slope, r^2- determination coefficient. The *p* values were obtained from SMA (standardized major axis) analyses, showing both original *p* values and *p* values adjusted after a Bonferroni correction for multiple comparisons. *p* values that reached the significance threshold of 0.05 after Bonferroni are in bold.

Trait	n	Female		Male		*p*	*p* (Bonferroni)
		b	r^2	b	r^2		
Pelvic Fin Width	90	1.276	0.971	0.997	0.961	0.000	**0.000**
Interocular Distance	91	1.130	0.950	0.966	0.966	0.002	**0.046**
Distance between the 1st pair of gill slits	90	1.167	0.985	1.061	0.979	0.002	0.051

TABLE 3 | Summary of the statistics for regressions of clasper traits *vs.* disc width (DW), comparing the developmental stages. n- number of analyzed specimens, *b*- slope, r^2- determination coefficient. The *p* values were obtained from SMA (standardized major axis) analyses, showing both original *p* values and *p* values adjusted after a Bonferroni correction for multiple comparisons. *p* values that reached the significance threshold of 0.05 after Bonferroni are in bold.

Trait	n	Juvenile		Adult		*p*	*p* (Bonferroni)
		b	r^2	*b*	r^2		
Clasper external length	60	2.472	0.727	0.828	0.579	0.000	**0.000**
Clasper internal length	59	1.884	0.720	1.016	0.802	0.000	**0.000**

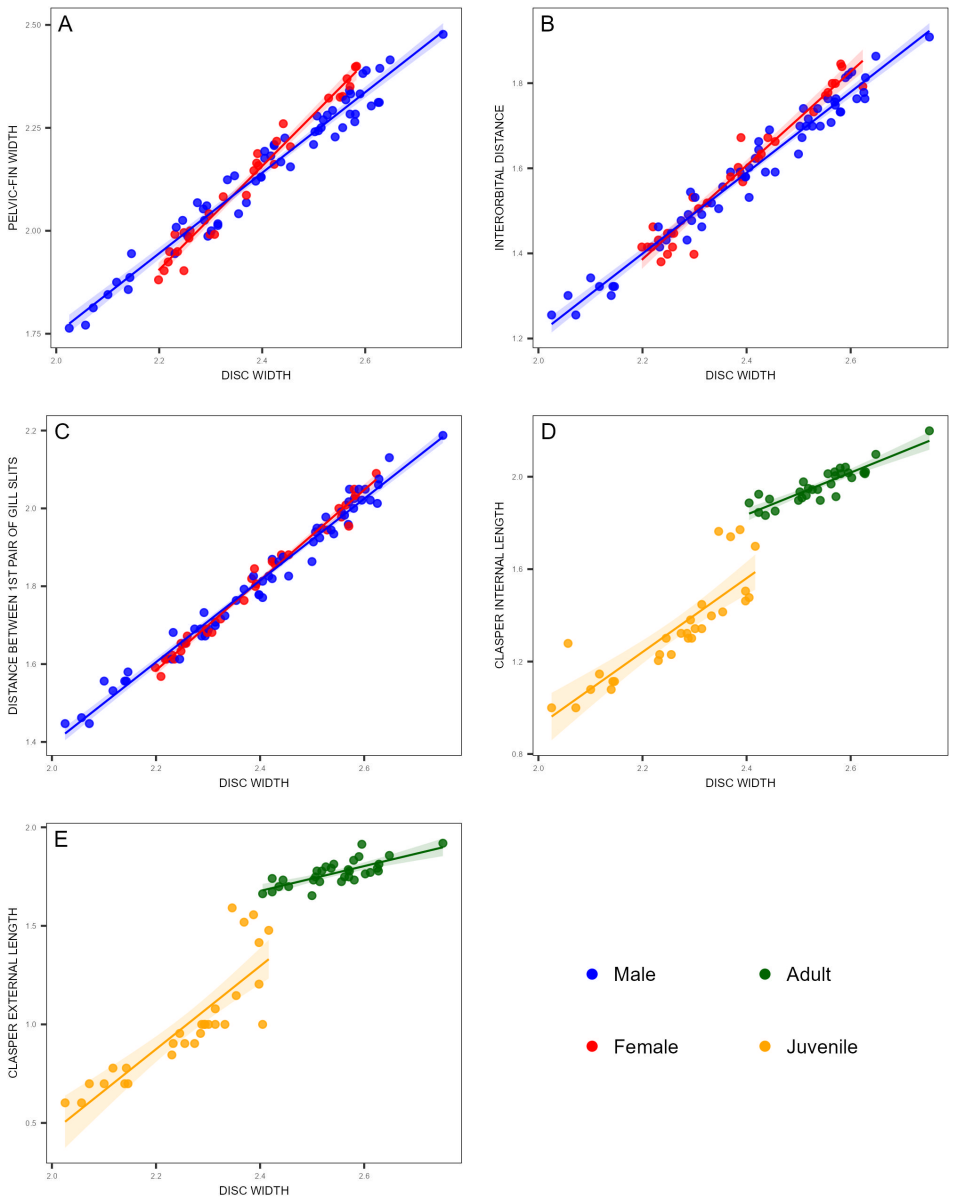

FIGURE 2 | Regressions of log-transformed traits *vs.* log-transformed disc width (DW) that present allometric differences in *Potamotrygon motoro*. Red: females, blue: males, yellow: juveniles, green: adults.

Finally, the analysis of clasper measurements in juvenile and adult males revealed distinct allometric patterns. Juveniles exhibited strong positive allometry in both external and internal clasper lengths (b = 2.172, and b = 1.884, respectively), indicating that these structures grow 2.986 and 1.854 times faster than the body size (DW) during this developmental stage. In contrast, adults displayed near-isometric growth (b = 0.828, and b = 1.016, respectively), suggesting a slowdown in clasper growth relative to body size after maturation (Tab. 3; Fig. 2).

Material examined. *Potamotrygon motoro*. Lectotype. NMW 78655, male, 215 mm DW, Brazil, Mato Grosso, rio Guaporé, 1830, Natterer. Paralectotype. ZMB 4662, female, 199 mm DW, Brazil, Mato Grosso, Cuiabá. **Argentina:** NMW 87239, female, 198 mm DW, Purna, 1904. NMW 88291a, female, 247 mm DW, La Plata, Jan 1884, Steindachner. NMW 88291b, female, 381 mm DW, La Plata, Jan 1884, Steindachner. ZMB 21918, female, 372 mm DW, Santa Fé, rio Paraná, 1969, M. N. Castex & H. P. Castello. **Bolivia:** MNHN 1988-809, male, 564 mm DW, Chaparez, Jun 1982. MNHN 1988-810, female, 360 mm DW, Lago Okiani, 14 Dez 1982, Lauzanne. MNHN 1988-1957, female, 170 mm DW, Itenez, Boca Machupo, 6 Sep 1984, Lauzanne & Loubens. **Brazil:** INPA 37445a, female, 177 mm DW, São Sebastião do Uatumã, rio Uatumã, 20 Sep 2011, SISBIOTA - Jatapu. INPA 37445b, female, 222 mm DW, São Sebastião do Uatumã, rio Uatumã, 20 Sep 2011, SISBIOTA - Jatapu. INPA 37445c, male, 114 mm DW, São Sebastião do Uatumã, rio Uatumã, 20 Sep 2011, SISBIOTA - Jatapu. INPA 37448, male, 193 mm, São José do Jabuti, rio Uatumã, 28 Sep 2011, SISBIOTA - Jatapu. INPA 37449, male, 409 mm DW, São José do Jabuti, rio Uatumã, 28 Sep 2011, SISBIOTA - Jatapu. MNHN A.1003, male, 323 mm DW, Caldeirão, Jobert. MNHN A.1004, female, 420 mm DW, Caldeirão, Jobert. MNHN 1988-807, male, 196 mm DW, lagoa Santa Rosa, 24 Sep 1983, Lauzanne. MNHN 1988-808, female, 245 mm DW, lagoa Santa Rosa, 29 Sep 1983, Lauzanne. NMW 78061, female, 356 mm DW, 1903. NMW 88291c, male, 394 mm DW, Amazonas, Jaturana, Jan 1884, Steindachner. ZMH 4197b, male, 170 mm DW, Amazonas, May 1969, Armbrüst & Birtholz. **Colombia:** CZUT-IC 3426a, male, 65 mm DW, Vichiuda, rio Inirida, 19 Feb 2006, C. Lasso *et al*. CZUT-IC 3426b, male, 64 mm DW, Vichiuda, rio Inirida, 19 Feb 2006, C. Lasso *et al*. IAvH 2887, male, 365 mm DW, Vaupes, rio Apapores, Lago Taraira, 1990, H. Lopez. IAvH 4582, male, 348 mm DW. IAvH 4683, male, 344 mm DW. IAvH 4725-1, male, 273 mm DW. IAvH 11884, female, 242 mm DW. IAvH 11891, male, 278 mm DW. IAvH 11892, female, 276 mm DW. IAvH 11896, male, 400 mm DW. IAvH uncat., male, 422 mm DW. IAvH uncat., male, 424 mm DW. IAvH uncat., male, 381 mm DW. IAvH uncat., male, 194 mm DW. IAvH uncat., female, 338 mm DW. IAvH uncat., male, 360 mm DW. IAvH uncat., male, 373 mm DW. IAvH uncat., male, 372 mm DW. IAvH uncat., female, 203 mm DW. IAvH uncat., female, 177 mm DW. IAvH uncat., male, 250 mm DW. IAvH uncat., female, 265 mm DW. IAvH uncat., male, 226 mm DW. IAvH uncat., male, 250 mm DW. IAvH uncat., male, 188 mm DW. IAvH uncat., male, 206 mm DW. IAvH uncat., male, 200 mm DW. IAvH uncat., male, 336 mm DW. IAvH uncat., male, 330 mm DW. IAvH uncat., male, 321 mm DW. IAvH uncat., male, 380 mm DW. IAvH uncat., male, 389 mm DW. IAvH uncat., male, 445 mm DW. IAvH uncat., male, 425 mm DW. IAvH uncat., male, 180 mm DW. IAvH uncat., female, 172 mm DW. IAvH uncat.,

female, 165 mm DW. IAvH uncat., male, 197 mm DW. IAvH uncat., male, 206 mm DW. IAvH uncat., male, 118 mm DW. IAvH uncat., female, 158 mm DW. IAvH uncat., female, 162 mm DW. IAvH uncat., male, 327 mm DW. IAvH uncat., male, 371 mm DW. IAvH uncat., male, 265 mm DW. IAvH uncat., male, 244 mm DW. IAvH uncat., female, 234 mm DW. IAvH uncat., female, 246 mm DW. IAvH uncat., female, 268 mm DW. IAvH uncat., male, 318 mm DW. IAvH uncat., female, 211 mm DW. IAvH uncat., male, 234 mm DW. IAvH uncat., male, 254 mm DW. IAvH uncat., male, 176 mm DW. ICN 4383, male, 139 mm DW, Amazonas, Letícia, Laguna Yahivaria, Nov 1979, M. Santos & S. Vijarano. ICN 12207, male, 126 mm DW, Guainia, Porto Inirida, Centro de Acopio, Feb 2005, Proyecto Ornamentales del Orinoco. ICN 12209, male, 106 mm DW, Guainia, Porto Inirida, Centro de Acopio, Feb 2005, Proyecto Ornamentales del Orinoco. ICN 12973, male, 316 mm D. **Guyana:** ZMB 4661, male, 254 mm DW, Schomburgk. **Paraguay:** BMNH 1892.12.29.1-2, female, 182 mm DW, Asuncion, rio Paraguay, Usher. BMNH 1935.6.4.4, female, 181 mm DW, Asuncion, rio Paraguay. ZMB 12497, male, 171 mm DW, R. Rohde. **Peru:** IIAP uncat., male, 140 mm DW. IIAP uncat., male, 138 mm DW. MUSM 6828, male, 285 mm DW, Loreto, Río Pacuya, Estación de Pesquería, Canal Puinahua, 05°07'S 74°25'W, 25 May 1960, H.W. Koepcke. MUSM 8239, female, 367 mm DW, Tambopata, Río Madre de Dios, Lago Valencia, 22 Oct 1995, F. Chang. MUSM 9967, male, 261 mm DW, Madre de Dios, Tambopata, Río Madre de Dios, Lago Valencia, 12°28'08"S 68°48'30"W, 18 May 1996, F. Chang. MUSM 11850, female, 383 mm DW, Carabaya, Río Candamo, 27 Aug 1997, F. Chang & N. Saludo. MUSM uncat., female, 285 mm DW. MUSM uncat., female, 265 mm DW. MUSM uncat., male, 131 mm DW. **Venezuela:** ZMH 123458a, male, 166 mm DW, Río Orinoco, Nov 1990, H. Bleher.

DISCUSSION

Overall, we found that females of *P. motoro* have eyes and the first pair of gill slits more widely spaced than males. These differences may be related to viviparity and its anatomical adaptations: *Potamotrygon* females are viviparous (Carvalho *et al*., 2003; Rosa *et al*., 2010), which is reflected in body cavity rearrangement for vitellogenesis and greater maternal metabolic investment (Walker, 2005; Conrath, Musick, 2012; Martins *et al*., 2015). Thus, the differences found might reflect the general cavity rearrangements that enable fetus development.

Another finding is related to the pelvic fins, as females exhibit broader pelvic fins, characteristic likely influenced by the overall form of such fins in the absence of clasper structures. These differences in pelvic-fin growth patterns may influence the swimming kinematics of stingrays.

Although the role of pectoral fins in swimming is well-documented in batoids, pelvic fins are crucial for locomotion in potamotrygonins, but have been much less studied (Shibuya *et al*., 2015). They are essential for swimming and body maneuvers, particularly during benthic locomotion (Lucifora, Vassallo, 2002; Macesic *et al*., 2013; Shibuya *et al*., 2015). Shibuya *et al*. (2015) provide a detailed analysis of the pelvic fins of *P. motoro*, concluding that the observed movements reflect advanced control and coordination of the pelvic musculature, enabling broader movements compared to other ray species.

Macesic *et al*. (2013) studied the movement of *P. orbignyi*, emphasizing its punting locomotion: a forward movement that includes a thrust followed by a glide/recovery phase, using the pelvic fins for support when thrusting. Both works extensively address the kinematics and morphological aspects of pelvic fins; however, they only studied juveniles. While Shibuya *et al*. (2015) used male specimens, Macesic *et al*. (2013) did not specify the sex of their subjects. Since our study indicates that pelvic fin growth patterns differ between sexes, it would be interesting to investigate whether these differences are reflected in pelvic fin kinematics.

Also, despite not finding statistically significant measurements between juvenile and adults of general body and head traits, the clasper results are extremely interesting because they grow 1.85 to 2.99 times faster in juveniles. The distinct allometric patterns between juveniles and adults suggest that claspers undergo significant morphological changes during development, potentially related to reproductive maturation. The strong positive allometry in juveniles may reflect accelerated growth of reproductive structures during early life stages, while the negative allometry in adults could indicate stabilization of clasper size after reaching functional maturity. Interestingly, Moreira *et al.* (2018) indicated that smaller species of *Potamotrygon*, such as *P. magdalenae* and *P. yepezi*, as well as *Plesiotrygon nana*, possess the largest claspers in percentages of disc width (%DW) of all analyzed potamotrygonin in their work. Thus, given our findings, it may be possible that those smaller species of *Potamotrygon* retain paedomorphic characteristics not only in overall size, but also in clasper relative size. Therefore, in this context, the allometric data can be used to infer heterochrony, as change in rates or timing of developmental processes are related to evolutionary changes (following Kingenberg, 1998). These findings highlight the importance of considering developmental stages, and the challenges of defining clear boundaries between life stages when studying morphological traits in elasmobranchs.

Considering all the results presented, we conclude that, despite its limited use, allometry plays a crucial role in understanding morphological variation in *P. motoro*. Some measurements commonly used in taxonomic descriptions are subject to different growth patterns between sexes and throughout ontogenetic development, suggesting that allometric differences must be considered when describing species. By investigating how different parts of the body relate and grow relative to each other, allometry reveals objective and quantifiable patterns that allow for a more precise characterization of species-specific traits. In this way, allometric analyses provide a refined understanding of evolutionary changes over time, highlighting a form of conservatism that is particularly useful for taxonomic delimitation.

Furthermore, with established allometric relationships, it becomes possible to predict certain characteristics of an organism based on known measurements. This is especially valuable for analyzing traits that are difficult to assess or for studying damaged specimens. Finally, we recommend the broader application of allometric analyses to freshwater stingrays of the genus *Potamotrygon*, not only to elucidate their taxonomy but also to deepen our understanding of aspects related to their ecomorphology and movement kinematics. Such studies could provide valuable insights into the evolutionary and ecological adaptations of this diverse and ecologically important group.

Finally, in this study we opted to discuss results that associate an alpha value more permissive to type-I error rate (10%) after applying the Bonferroni correction for

multiple comparisons, when associated to a high determination coefficient ($r^2 > 0.8$). Although the usage of such alpha is not standard, this study has an exploratory nature on the growth patterns of potamotrigonins and is the first to address such patterns based on statistical analyses. However, we are limited by the naturally reduced sample size of individuals available for morphological analyses, and we believe type-II errors (false negatives) are as problematic as type-I errors (false positives) when we deal with our kind of biological data. Also, the determination coefficient of most analyzed traits was superior to 0.7, suggesting the allometric differences found correspond to consistent biological patterns, and not mere statistical artifacts (see Nakagawa, 2004 and Nakagawa, Cuthill, 2007 for comments on solutions related to low statistical power in biological sciences).

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REFERENCES

- **Alberch P, Gould SJ, Oster GF, Wake DB.** Size and shape in ontogeny and phylogeny. Paleobiology. 1979; 5(3):296–317. https://doi.org/10.1017/S0094837300006588
- **Atchley WR.** Ontogeny, timing of development, and genetic variance-covariance structure. Am Nat. 1984; 123(4):519–40. https://doi.org/10.1086/284220
- **Bigelow HB, Schroeder WC.** Sharks, sawfishes, guitarfishes, skates and rays. Chimaeroids. In: Tee-Van J, Breder CM, Hildebrand SM, Parr AE, Schroeder WC, editors. Fishes of the Western North Atlantic. Part 2. New Haven: Sears Foundation for Marine Research, Yale University; 1953. p.1–514.
- **Carvalho MR.** *Potamotrygon rex*, a new species of neotropical freshwater stingray (Chondrichthyes: Potamotrygonidae) from the middle and upper rio Tocantins, Brazil, closely allied to *Potamotrygon henlei* (Castelnau, 1855). Zootaxa. 2016; 4150(5):537–65. https://doi.org/10.11646/zootaxa.4150.5.2
- **Carvalho MR, Lovejoy NR, Rosa RS.** Family Potamotrygonidae (river stingrays). In: Reis RE, Kullander SO, Ferraris CJ Jr., editors. Check list of the freshwater fishes of South and Central America. Porto Alegre: Edipucrs; 2003. p.22–28.
- **Carvalho MR, Perez MHS, Lovejoy NR.** *Potamotrygon tigrina*, a new species of freshwater stingray from the upper Amazon basin, closely related to *Potamotrygon schroederi* Fernandez-Yépez, 1958 (Chondrichthyes: Potamotrygonidae). Zootaxa. 2011; 2827(1):1–30. https://doi.org/10.11646/zootaxa.2827.1
- **Chandler CR.** Practical considerations in the use of simultaneous inference for multiple tests. Anim Behav. 1995; 49(2):524–27. https://doi.org/10.1006/anbe.1995.0069
- **Cheverud JM, Rutledge JJ, Atchley WR.** Quantitative genetics of development: genetic correlations among age-specific trait values and the evolution of ontogeny. Evolution. 1983; 37(5):895–905. https://doi.org/10.2307/2408405

- **Citeli N, Klaczko J, De-Lima AKS, De-Carvalho M, Nunes PMS, Passos P *et al*.** Taxonomy, allometry, sexual dimorphism, and conservation of the trans-Andean watersnake *Helicops danieli* Amaral, 1937 (Serpentes: Dipsadidae: Hydropsini). Can J Zool. 2022; 100(3):184–96. https://doi.org/10.1139/cjz-2021-0073
- **Cock AG.** Genetical aspects of metrical growth and form in animals. Q Rev Biol. 1966; 41(2):131–90. https://doi.org/10.1086/404940
- **Compagno LJV, Cook SD.** The exploitation and conservation of freshwater elasmobranches: status of taxa and prospects for the future. In: Oetinger MI, Zorzi GD, editors. The biology of freshwater elasmobranchs, a symposium to Honor Thomas B. Thorson. Urbana: Journal of Aquariculture & Aquatic Sciences, vol. VII; 1995. p.62–90.
- **Conrath CL, Musick JA.** Reproductive biology of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR, editors. Biology of sharks and their relatives. Boca Raton: CRC press; 2012. p.291–312.
- **Csárdi G, FitzJohn R.** progress: terminal progress bars [Internet]. R package version 1.2.3; 2023. Available from: https://CRAN.R-project.org/package=progress
- **Fontenelle JP, Silva JPCB, Carvalho MR.** *Potamotrygon limai*, sp. nov., a new species of freshwater stingray from the upper Madeira River system, Amazon basin (Chondrichthyes: Potamotrygonidae). Zootaxa. 2014; 3765(3):249–68. https://doi.org/10.11646/zootaxa.3765.3.2
- **Fontenelle JP, Carvalho MR.** Systematic revision of the *Potamotrygon scobina* Garman, 1913 species-complex (Chondrichthyes: Myliobatiformes: Potamotrygonidae), with the description of three new freshwater stingray species from Brazil and comments on their distribution and biogeography. Zootaxa. 2017; 4310(1):1–63. https://doi.org/10.11646/zootaxa.4310.1.1
- **Fontenelle JP, Marques FPL, Kolmann MA, Lovejoy NR.** Biogeography of the Neotropical freshwater stingrays (Myliobatiformes: Potamotrygoninae) reveals effects of continent-scale paleogeographic change and drainage evolution. J Biogeogr. 2021; 48(6):1406–19. https://doi.org/10.1111/jbi.14086
- **Fox J, Weisberg S.** An R companion to applied regression. Third edition. New York: Sage Publications; 2019.
- **Fricke R, Eschmeyer WN, Van der Laan R.** Eschmeyer's catalog of fishes: genera, species, references [Internet]. San Francisco: California Academy of Sciences; 2026. Available from: http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp
- **Gould SJ.** Allometry and size in ontogeny and phylogeny. Biol Rev. 1966; 41(4):587–638. https://doi.org/10.1111/j.1469-185X.1966.tb01624.x
- **Gould SJ.** Geometric similarity in allometric growth: a contribution to the problem of scaling in the evolution of size. Am Nat. 1971; 105:113–36. https://doi.org/10.1086/282710
- **Huxley JS.** Constant differential growth-ratios and their significance. Nature. 1924; 114(2877):895–96.
- **Huxley JS, Teissier G.** Terminology of relative growth. Nature. 1936; 137:780–81. http://dx.doi.org/10.1038/137780b0
- **Jolicoeur P.** The multivariate generalization of the allometry equation. Biometrics. 1963; 19(3):497–99. https://doi.org/10.2307/2527939
- **Klingenberg CP.** Heterochrony and allometry: the analysis of evolutionary change in ontogeny. Biol Rev. 1998; 73(1):79–123. https://doi.org/10.1017/S000632319800512X
- **Klingenberg CP.** Size, shape, and form: concepts of allometry in geometric morphometrics. Dev Genes Evol. 2016; 226(3):113–37. https://doi.org/10.1007/s00427-016-0539-2
- **Klingenberg CP, Zimmermann M.** Static, ontogenetic, and evolutionary allometry: a multivariate comparison in nine species of water striders. Am Nat. 1992; 140(4):601–20. https://doi.org/10.1086/285430
- **Lasso CA, Rosa RS, Sánchez-Duarte P, Morales-Betancourt MA, Agudelo-Córdoba E.** IX. Rayas de agua dulce (Potamotrygonidae) de Suramérica Parte I: Colombia, Venezuela, Ecuador, Perú, Brasil, Guyana, Surinam y Guayana Francesa: diversidad, bioecología, uso y conservación. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; 2013.

- **De-Lima AKS, Paschoaletto IP, Pinho LDO, Benmamman P, Klaczko J.** Are hemipenial traits under sexual selection in *Tropidurus* lizards? Hemipenial development, male and female genital morphology, allometry and coevolution in *Tropidurus torquatus* (Squamata: Tropiduridae). PLoS ONE. 2019; 14(7):e0219053. https://doi.org/10.1371/journal.pone.0219053
- **Loboda TS.** Revisão taxonômica e morfológica de *Potamotrygon motoro* (Müller & Henle, 1841) na bacia Amazônica (Chondrichthyes: Myliobatiformes: Potamotrygonidae). [Master Thesis]. São Paulo: Universidade de São Paulo; 2010. Available from: https://www.teses.usp.br/teses/disponiveis/41/41133/tde-08122010-112151/publico/ThiagoLoboda.pdf
- **Loboda TS, Carvalho MR.** Systematic revision of the *Potamotrygon motoro* (Müller & Henle, 1841) species complex in the Paraná-Paraguay basin, with description of two new ocellated species (Chondrichthyes: Myliobatiformes: Potamotrygonidae). Neotrop Ichthyol. 2013; 11(4):693–737. https://doi.org/10.1590/S1679-62252013000400001
- **Lucifora LO, Vassallo AI.** Walking in skates (Chondrichthyes, Rajidae): anatomy, behaviour and analogies to tetrapod locomotion. Biol J Linn Soc. 2002; 77(1):35–41. https://doi.org/10.1046/j.1095-8312.2002.00085.x
- **Macesic LJ, Mulvaney D, Blevins EL.** Synchronized swimming: coordination of pelvic and pectoral fins during augmented punting by the freshwater stingray *Potamotrygon orbignyi*. Zoology. 2013; 116(3):144–50. https://doi.org/10.1016/j.zool.2012.11.002
- **Martins AP, Silva Filho E, Feitosa LM, Silva LPN, Almeida ZS, Nunes JLS.** Sexual dimorphism of sharks from the Amazonian equatorial coast. Univ Sci. 2015; 20(3):297–304. https://doi.org/10.11144/Javeriana.SC20-3.sdos
- **Moreira RA, Loboda TS, Carvalho MR.** Comparative anatomy of the clasper of the subfamily Potamotrygoninae (Chondrichthyes: Myliobatiformes). Morphology. 2018; 279(5):598–608. https://doi.org/10.1002/jmor.20795
- **Müller K, Wickham H.** tibble: simple data frames [Internet]. R, package version 3.2.1; 2023. Available from: https://CRAN.R-project.org/package=tibble
- **Nakagawa S.** A farewell to Bonferroni: the problems of low statistical power and publication bias. Behav Ecol. 2004; 15(6):1044–45. https://doi.org/10.1093/beheco/arh107
- **Nakagawa S, Cuthill IC.** Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol Rev. 2007; 82(4):591–605. https://doi.org/10.1111/j.1469-185X.2007.00027.x
- **R Development Core Team.** R: a language and environment for statistical computing [Internet]. Vienna: R Foundation for Statistical Computing; 2023. Available from: https://www.R-project.org/
- **Rice WR.** Analyzing tables of statistical tests. Evolution. 1989; (43):223–25. https://doi.org/10.2307/2409177
- **Rincon G, Soares CES, Wosnick N, Nunes J.** Dimorfismo sexual da raia de água doce *Potamotrygon motoro* dos lagos de Viana, Maranhão. In: Oliveira Jr. JMB, Calvão LB, editors. Tópicos integrados de zoologia. Ponta Grossa: Editora Atena; 2019. p.15–25. https://doi.org/10.22533/at.ed.1471915102
- **Rosa RDS.** A systematic revision of the South American freshwater stingrays (Chondrichthyes: Potamotrygonidae) (Batoidei, Myliobatiformes, phylogeny, biogeography). [PhD Dissertation]. The College of William and Mary; 1985. Available from: https://dx.doi.org/doi:10.25773/v5-6ts0-6v68
- **Rosa RS, Charvet-Almeida P, Quijada CCD.** Biology of the South American potamotrygonid stingrays. In: Carrier JC, Musick JA, Heithaus MR, editors. Sharks and their relatives II: biodiversity, adaptive physiology, and conservation. Boca Raton: CRC Press; 2010. p.241–85. https://doi.org/10.1201/9781420080483-c5
- **RStudio Team.** RStudio: integrated development environment for R [Internet]. Posit Software, PBC; 2016. Available from: https://posit.co
- **Shibuya A, Carvalho MR, Zuanon J, Tanak, S.** The use of pelvic fins for benthic locomotion during foraging behavior in *Potamotrygon motoro* (Chondrichthyes: Potamotrygonidae). Zoologia. 2015; 32(3):179–86. https://doi.org/10.1590/S1984-46702015000300001

- **Shingleton A.** Allometry: the study of biological scaling [Internet]. Nature Education Knowledge; 2010. Available from: https://www.nature.com/scitable/knowledge/library/allometry-the-study-of-biological-scaling-13228439/
- **Silva JPC, Carvalho MR.** A new species of Neotropical freshwater stingray of the genus *Potamotrygon* Garman, 1877 from the Río Madre de Díos, Peru (Chondrichthyes: Potamotrygonidae). Pap Avulsos Zool. 2011a; 51(8):139–54. https://doi.org/10.1590/S0031-10492011000800001
- **Silva JPC, Carvalho MR.** A taxonomic and morphological redescription of *Potamotrygon falkneri* Castex & Maciel, 1963 (Chondrichthyes: Myliobatiformes: Potamotrygonidae). Neotrop Ichthyol. 2011b; 9(1):209–32. https://doi.org/10.1590/S1679-62252011000100021
- **Smith JM, Burian R, Kauffman S, Alberch P, Campbell J, Goodwin B *et al*.** Developmental constraints and evolution: a perspective from the Mountain Lake conference on development and evolution. Q Rev Biol. 1985; 60(3):265–87. https://doi.org/10.1086/414425
- **Taniuchi T, Ishihara H.** Anatomical comparison of claspers of freshwater stingrays (Dasyatidae and Potamotrygonidae). Jpn J Ichthyol. 1990; 37(1):10–16. https://doi.org/10.11369/jji1950.37.10
- **Voje KL, Hansen TF.** Evolution of static allometries: adaptive change in allometric slopes of eye span in stalk-eyed flies. Evolution. 2014; 67(2):453–67. https://doi.org/10.1111/j.1558-5646.2012.01777.x
- **Wagiyo K, Kembaren DD, Noegroho T, Nugraha B, Hufiadi U, Chondriya *et al*.** Life history (length-weight relationship, conditional factors, reproductive aspects), stomach contents and nursery ground of stingray in the Arafura Sea. In: Setiawan A, Triyulianti I, Fretes CE, Tuakia MZ, Likumahua S, Hamzah F *et al*., editors. IOP Conference series: earth and environmental science. Alamos: IOP Publishing. 2023; 1163. https://doi.org/10.1088/1755-1315/1163/1/012009
- **Walker TI.** Reproduction in fisheries science. In: Hamlett WC, editor. Reproductive biology and phylogeny of Chondrichthyes. Sharks, batoids and chimaeras. Boca Raton: CRC Press. 2005. p.81–128. https://doi.org/10.1201/9781439856000
- **Warton DI, Duursma RA, Falster DS, Taskinen S.** smatr 3 – an R package for estimation and inference about allometric lines. Methods Ecol Evol. 2012; 3(2):257–59. https://doi.org/10.1111/j.2041-210X.2011.00153.x
- **Whitlock ML, Schluter D.** The analysis of biological data. Greenwood Village: Roberts Publishers; 2015.
- **Wickham H.** stringr: simple, consistent wrappers for common string operations. R, package version 1.5.1; 2023. Available from: https://CRAN.R-project.org/package=stringr
- **Wickham H, Bryan J.** readxl: read Excel files [Internet]. R, package version 1.4.3; 2023. Available from: https://CRAN.R-project.org/package=readxl
- **Wickham H, François R, Henry L, Müller K, Vaughan D.** dplyr: a grammar of data manipulation [Internet]. R, package version 1.1.4; 2023. Available from: https://CRAN.R-project.org/package=dplyr
- **Wickham H, Henry L.** purrr: functional programming tools [Internet]. R, package version 1.0.2; 2023. Available from: https://CRAN.R-project.org/package=purrr
- **Wickham H, Chang W, Henry L, Pedersen TL, Takahashi K, Wilke C *et al*.** ggplot2: create elegant data visualizations using the grammar of graphics [Internet]. R, package version 3.4.0; 2024a. Available from: https://CRAN.R-project.org/package=ggplot2
- **Wickham H, Vaughan D, Girlich M.** tidyr: tidy messy data [Internet]. R, package version 1.3.1; 2024b. Available from: https://CRAN.R-project.org/package=tidyr

AUTHORS' CONTRIBUTION

Júlia Papalardo Azevedo: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing-original draft, Writing-review and editing.

Thiago Silva Loboda: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Supervision, Validation, Writing-original draft, Writing-review and editing.

Veronica Slobodian: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

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ETHICAL STATEMENT

Not applicable.

DATA AVAILABILITY STATEMENT

The datasets generated during the current study are available in the Figshare repository, DOI: 10.6084/m9.figshare.30251551.

AI STATEMENT

The authors used DeepSeek, an AI-powered language model, for improving the English language and clarity of this manuscript. The authors also used Julius, an AI-powered language model, to troubleshooting R script analyses.

COMPETING INTERESTS

The authors declare no competing interests.

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