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Research paper

Sexual dimorphism, ontogeny and static allometry of a semi-fossorial snake (genus *Atractus*)

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ABSTRACT

Sexual dimorphism in snakes has been mainly evaluated for size and number of some morphological traits, but few studies address on sexual shape dimorphism. Here we evaluated the existence of sexual size and shape dimorphism in the semi-fossorial snake *Atractus reticulatus*. We use linear and geometric morphometrics to evaluate differences between sexes and among different ontogenetic stages (neonates, juveniles and adults). We have shown that *A. reticulatus* is sexually dimorphic for some traits such as body length and head shape, with females being larger and having more robust heads than males, but the sexes do not differ in head size. Males and females are sexually dimorphic in head shape even in neonates, suggesting that this differentiation is prenatal. Differences in head shape may be associated with trophic segregation, allowing females to feed on larger prey than males. Body size dimorphism progressively increases throughout the ontogenetic stages, which is possibly related to the late sexual maturation of females and/or different growth rates between the sexes. We also found that males and females shows some sex-specific patterns towards static and ontogenetic allometry, with males showing stronger predictive response on static allometry than females, whereas females have ontogenetic allometry, but males do not. Additionally, the allometric slopes in *A. reticulatus* between sexes converge by presenting similar shapes as head size increases, an expected result for sexes with similar lifestyles. Further investigation on some physiological and natural history aspects in *Atractus* will be particularly useful for a better understanding of the significance of the morphological differences found in this study.

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1. Introduction

Intraspecific variation is the primary component of the evolution through natural selection (Darwin 1859; Van Valen 1965). Several factors may regulate such variability (e.g., gene flow or vicariant events, niche segregation and sexual selection) (Shine 1978; Perry 1996; Leaché et al. 2009). For instance, sexual selection imposes differential pressures between sexes, since the reproductive success of males and females are guided in different spectra of the phenotypic space. As a result, most animals exhibit some level of secondary sexual dimorphism (Bradbury & Anderson 1987; Lovich & Gibbons 1992). In snakes, secondary sexual dimorphism can be observed in the number and ornamentation of scales, head, body and tail size, mass, colour patterns, and hard and soft anatomy (Keogh & Wallach 1999; Campbell & Lamar 2004; Manier 2004; Murta-Fonseca et al., 2019). In general, adult females tend to have larger body and head sizes than males (Shine 1978). The current paradigm in evolutionary ecology argues that, by increasing the size, female can store more energy through adipose tissues and, consequently, larger females are able to generate numerous offsprings (Bonnet et al. 1998). In contrast, the sexual

dimorphism of snake head size and shape is less understood, although some hypotheses have been raised on this issue (Camilleri & Shine 1990).

Head size in snakes does not appear to be guided by sexual selection, as explaiations for this difference come mainly from dietary preferences. In this context, males and females would consume different prey types or even when of different age class-ess, reducing intraspecific competition for food resources (Shine 1991). Additionally, head size sexual dimorphism may be an acci-dental consequence of heterochronic processes related to gene regulation modulating hormones expression during ontogeny. For example, in the sense that shorter jaw length (related to head size) in males may be caused by inhibition of head growth by testicular androgens (Shine & Crews 1988). Yet while some species progres-sively develop sexually dimorphic heads after birth (Smith 2014), others are born with sexually distinct heads, indicating that the allometric ontogenetic signal may be initiated prenatal (Shine & Crews 1988; Camilleri & Shine 1990). Meanwhile, sexual shape dimorphism has been poorly investigated in snakes, especially in the light of ontogenetic allometry, and studies addressing sexual differences in neonates and juveniles are astonishing scarce (Tomović et al. 2010; Silva et al. 2017). In geometric morphometric approaches, specifically for adult specimens, sexual dimorphism in the head size of snakes is commonly found (Tamagnini et al. 2018; Loebens et al. 2019), while for head shape it has only been found for some species (Meik et al. 2012; Tamagini et al. 2018; Murta-Fonseca et al. 2019). In Tachymenini snakes, such as Thamnodynastes stri-gatus (Günther, 1858) and Tomodon dorsatus Duméril, Bibron & Duméril, 1854, females present an enlargement either of the pari-etal region or of the snout, respectively, when compared to males. These features may indicate that females tend to consume larger preys than males, without necessarily displaying sexual dimor-phism in head size, at least for T. strigatus (Loebens et al., 2019).

Allometry—the size-related changes of morphological traits—is one of the main attributes of the morphological variation among different animal lineages (e.g., Gould 1966; Meyer 1990; Knigge et al. 2015; Klingenberg 2016). At least three types of allometry can be recognized (Cock 1966; Klingenberg 1998): evolutionary allometry—deals with morphological variation on phylogenetic lineages by analyzing equivalent semaphoronts; ontogenetic allo-metry—in which morphology varies with growth; and static allo-metry—compares morphological traits between individuals at the same ontogenetic stage. Through the application of traditional morphometric methods (= linear morphometry), most studies on the subject have focused on the morphological variation associated with ontogenetic changes in the diet, which are related to changes in the feeding apparatus of a species (Rossman 1980; Vincent et al., 2004; Schuett et al., 2005; Natusch & Lyons 2012; López et al. 2013; Hampton 2014). On one hand, Murta-Fonseca & Fernandes (2016) explored the ontogenetic allometry of the skull of Hydrodynastes gigas (Duméril, Bibron & Duméril, 1854), and Silva et al. (2017) of the head shape of Bothrops atrox (Linnaeus, 1758), species of aquatic and terrestrial habits, respectively. Based upon geometric morphometry methods, it was verified that the skull and head shape of these species vary significantly from neonates to adults, even though the ecological implications of these changes remain unknown in most neotropical lineages, except perhaps for some species of Bothrops (Wüster et al., 2005; López et al., 2013 and references therein). Static allometric patterns were also found in snake's head shape, suggesting that size is not only associated to head shape changes during growth, but also in the size related differences between adult specimens as well. Tamagnini et al. (2018) found that in Natrix helvetica (Lacépède, 1789), a non-venomous active forager snake, there are reinforcement of fea-tures that may enhance bite force in larger specimens. By contrast,

such pattern were not observed in the venomous sit-and-wait sympatric Vipera berus (Linnaeus, 1758). The authors pointed out that envenomation of prey items may reduce the need for a stronger bite force in larger individuals. These studies were all conducted with taxa presenting terrestrial, semi-arboreal or semi-aquatic lifestyle, but never semi-fossorial. Squamata species with semi-fossorial habits use the anterior portion of their heads, mainly the snout region, for digging and underground locomoting, implying that functional related morphological constraint may apply in burrowing animals (Gans 1974; Savitzky 1983).

The genus Atractus Wagler, 1828 comprises semi-fossorial snakes that are widely distributed in the Neotropics, occurring from Panama to northeastern Argentina (Giraudo & Scrocchi 2000; Myers 2003). It is the world's most species-rich genus of snakes and includes about 150 species (Melo-Sampaio et al. 2019). This genus is included in the Central American Dipsadinae group denominate "goo-eaters" that feeds on soft-bodied invertebrates (Cadle & Greene 1993; Grazziotin et al. 2012). Atractus reticulatus (Boulenger, 1885) is a small species broadly distributed in the southern Paraguay, northeastern Argentina and southeastern and southern Brazil (Passos et al. 2010). There is sexual dimorphism in body size in this species, with females reaching larger snout-vent length and males larger tail length (Balestrin & Di-Bernardo 2005). This species is an active forager during the night and twi-light, being also a specialized earthworm hunter (Balestrin et al. 2007). Here, we combined linear and geometric morphometric techniques to investigate sexual dimorphism, ontogenic and static allometries in A. reticulatus. We assessed the following questions: (i) Is there sexual dimorphism in snout-vent length, head shape and size of A. reticulatus? (ii) Are there static and ontogenetic allome-tries in head shape? If so, (iii) Does size predict different percent-ages of shape variance between sexes? (iv) Does the enhancement of size select different traits in each sex that might contribute for sexual dimorphism?

2. Materials and methods

2.1. Data acquisition

Our sample includes 121 specimens of A. reticulatus (females = 59, males = 62) and the vouchers and localities are listed in Appendix I. The samples are from two different herpetological scientific collections: Coleção Herpetológica da Universidade Fed-eral de Santa Maria (ZUFSM) and Coleção Herpetológica do Museu de Ciências e Tecnologia, PUC-RS (MCP). Sex was verified by an incision at the base of the tail to check for the presence/absence of the hemipenis. We took the linear measurement of the snout-vent length (SVL) to the nearest mm. The age group of individuals fol-lowed the categories described in Balestrin & Di-Bernardo (2005): neonate males and females with umbilical scar (<117 mm SVL); immature males (117—198 mm SVL) and females (117—242 mm SVL); and mature males (>198 mm SVL) and females (above 242 mm SVL). We used a Nikon D600 digital camera with macro lens AF-S Micro-Nikkor 60 mm f/2.8G ED 60 mm. The head of each spec-imen was carefully positioned perpendicularly to the camera lens at fixed distance of 12 cm and photographed from above in dorsal view (see Tamagnini et at. 2018). We have excluded from our analyzed sample the damaged specimens (e.g., dried out individuals), with head deformations (e.g., broken cranium) or presenting preparation bias (e.g., open-mouth preserved specimens).

Each picture was digitally landmarked by one of us (ADA) using the tpsDig2 ver. 2.16 (Rohlf 2015). We chose 26 landmarks, that were easily recognizable in all specimens added in this study. For choosing the landmark configuration, we focused on describing the overall shape of the head, the eyes areas and positioning, and the

most recognizable shields (rostral, prefrontals, frontal and parietals). Our configuration of landmarks accounts for both sides of the head (Fig. 1, Table 1). We applied the Generalized Procrustes Analysis (GPA, Rohlf & Slice 1990) in the symmetric component of shape. GPA removes differences from the original landmarks that are unrelated to shape: scale (= centroid size), position, and orientation (Rohlf & Marcus 1993). Based on this procedure, we obtained our response variable, the Procrustes Coordinates for the symmetric component of head shape (= HSh, see Klingenberg et al. 2002), and size (= HS, as centroid size, Zelditch et al. 2012).

2.2. Statistical analyses

2.2.1. Adult sample

We tested for differences between sexes in head shape, HS and SVL using Procrustes ANOVA models with 9,999 permutations and computed morphological disparity within males and females (Adams & Otárola-Castillo 2013). To visualize the overall adult symmetric shape of our data, we performed a principal component analysis (PCA) of the Procrustes coordinates. Sexual dimorphism for each of the size variables were visualized using boxplots. Through two-way Procrustes ANOVA models, we tested for the interaction between sex and size in head shape (Adams et al. 2018). We performed multiple regression models to test for allometry in each sex separately to see if allometric strength is comparable between sexes and tested the allometric slopes for angular differences between sexes (Klingenberg 2011).

2.2.2. Ontogenetic sample

In the ontogenetic sample, we tested for the significance of age and sex in HSh, HS. SVL was only tested for sexual dimorphism because age-classes are categorized based on SVL values. Age-related differences and sexual dimorphism for each of the size variables were visualized using boxplot. An additional estimate of sexual size dimorphism (SSD) was obtained by subtracting the mean female and male centroid and SVL sizes for each ontogenetic age (see Tamagnini et al. 2018). Sexual shape dimorphism was computed as the Procrustes distance of the means of female and male shape coordinates in each ontogenetic age class. Procrustes distance is the square root of the sum of squared differences in positioning of landmarks between two shape configurations
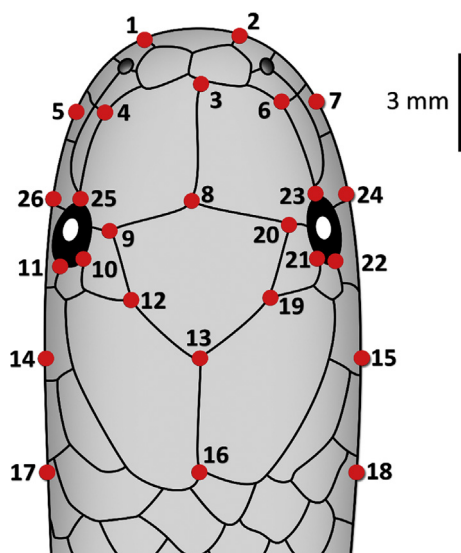
(Zelditch et al. 2012). The higher the Procrustes distance between female and male mean configurations in each age class, the higher the sexual dimorphism (see Astúa 2010 and Tamagnini et al. 2018 for similar approach). To test for the ontogenetic allometric signal we used SVL instead of HS as size variable. We chose SVL instead of HS because the growth of snakes is mearsured by this specific variable and not HS (Balestrin & Di-Bernardo 2005). HS, on the other hand, is more variable and frequently overlaps between age classes (see our results). We also analysed the relative trend of HS vs SVL in order to understand the relative HS variation during *A. reticulatus* ontogenetic growth across age classes in each sex. The strength of allometric signal, that is, the percentage of head shape which is predicted by size variation, was tested by performing a multivariate regression of head shape with SVL for each sex (Klingenberg, 2016).

2.3. Software used in the data analysis

The PCA analyses and regression models were performed in MorphoJ (Klingenberg 2011). Procrustes ANOVA models and morphological disparity were performed in R environment (R Core Team 2018), with the package 'geomorph' (Adams & Otárola-Castillo 2013).

3. Results

3.1. Adult sample

Sexual dimorphism was significant for head shape ($R^2 = 0.041$, $F_{1,87} = 3.725$, $P = 0.001$) and SVL ($R^2 = 0.523$, $F_{1,87} = 95.498$, $P < 0.001$), but not head size ($R^2 < 0.001$, $F_{1,87} < 0.001$, $P = 0.979$). The first two PCs summarized 47.26% or shape variation. Plotting them together, sexes are highly overlapped in head shape (Fig. 2). PC2 shows a slightly larger morphospace for males than females. This was supported by the morphological disparity values, which are slightly higher for males (Males MD: 0.0027 > Females MD: 0.0026). PC2 shows that males can achieve morphotypes of a proportionally slender head shape, with wider and more elongated prefrontal shield, and wider frontal shield (shape associated with negative PC2 scores at Fig. 2). The opposite shape deformation is present in both males and females (at positive PC2 scores, Fig. 2).

Boxplot clearly shows the lack of sexual dimorphism for the adult sample in head size and more variance in males head size (Fig. 3), supported by the morphological disparity values (Males MD: 0.0237 > Females MD: 0.0177). It also shows that SVL values in females are larger than in males (Fig. 3) but they are not notably higher in variance, despite detectable through morphological disparity (Females MD: 0.0053 > Males MD: 0.0035).

Two-way Procrustes ANOVA showed that adults have significant head shape variation associated with size ($R^2 = 0.071$, $F_{1,85} = 6.832$, $P = 0.001$) and that shape is different between sexes ($R^2 = 0.041$, $F_{1,85} = 3.955$, $P = 0.001$), but interaction between factors was not significant ($R^2 = 0.006$, $F_{1,85} = 0.591$, $P = 0.691$). The regression between shape and size (head size) separating sexes show a significant allometric slope for females (6.38%, $P = 0.021$) and males (% explained: 9.32%, $P < 0.001$). The angular comparison showed that the allometric pattern between males and females are convergent (data points occupy the same morphospace at the same regions of the plot), that is, different from a 90° angle (angle = 33.94°, $P < 0.001$). In summary, larger *A. reticulatus* specimens tend to have longer, but thinner prefrontal shields, smaller frontal shields with a diamond shape and proportionally wider orbital opening (see discussion). Eyes are at a more caudal position in larger specimens, compared with smaller specimens. Comparing the smaller specimen's deformations, females have shorter and wider head than males (Fig. 4).

Fig. 1. Morphological landmarks used to describe *Atractus reticulatus* head shape.

Table 1
Description of each landmark positioning.

| Number of landmark	Description
1	Left contact between nasals and rostral
2	Right contact between nasals and rostral
3	External contact point between prefrontals and internasals
4	Left external angle of prefrontal
5	External left point from landmark 4
6	Right external angle of prefrontal
7	External right point from landmark 6
8	Anterior external contact point between prefrontals and frontal
9	Left external contact point between prefrontal, frontal and supraocular
10	Nearest contact point to the eye between supraocular and postocular
11	Nearest contact point to the eye between left postocular and supralabials
12	Left contact point between supraocular, frontal and parietal
13	External posterior contact point between parietals and frontal
14	Straight point in right temporal shield from mark 13
15	Straight point in left temporal shield from mark 13
16	External posterior contact point between parietals
17	Straight lateral left point from landmark 16
18	Straight lateral right point from landmark 16
19	Right contact point between supraocular, frontal and parietal
20	External contact point of prefrontal, frontal and supraocular
21	Nearest contact point to eye between supraocular and postocular
22	Nearest contact point to eye between right postocular and supralabials
23	Anterior right external point of ocular cavity
24	Straight external right point from landmark 23
25	Anterior left external point of ocular cavity
26	Straight external left point from landmark 25
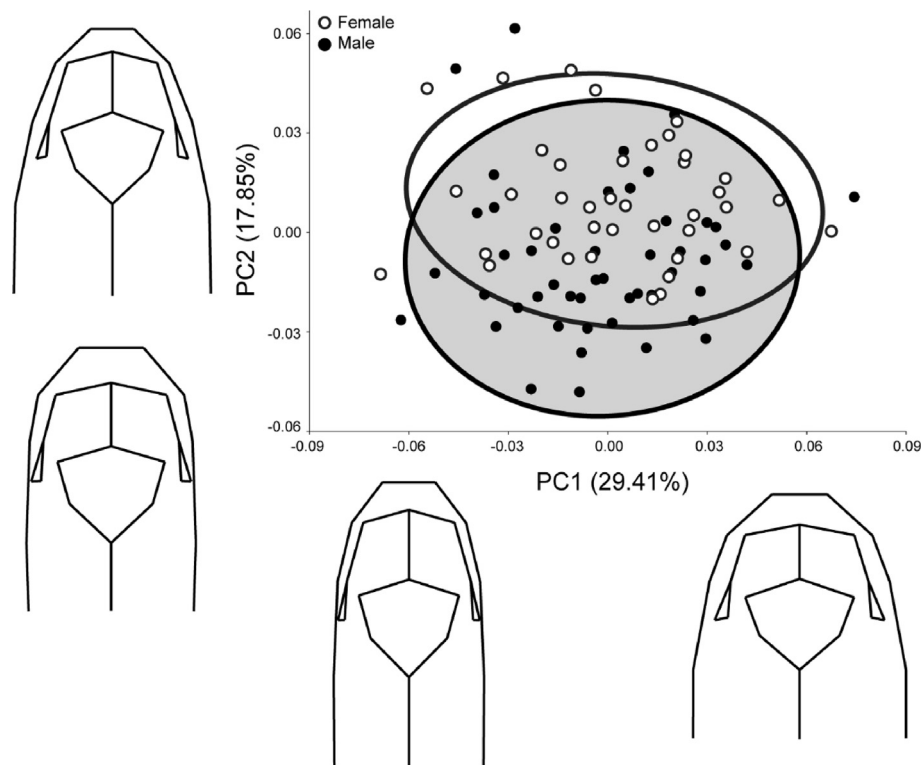
Fig. 2. Scatter plot of PC1 versus PC2 of head shape variation of *Atractus reticulatus*. Visualize shape deformations relative to the mean at the positive and negative extremes of each principal component. Symbols are coloured by sex, a key is provided.

3.2. Ontogenetic sample

We found significant differences for sexual dimorphism in head shape ($R^2 = 0.018$, $F_{1, 119} = 2.162$, $P = 0.037$), and SVL ($R^2 = 0.055$, $F_{1, 119} = 6.911$, $P = 0.009$), but not for head size ($R^2 < 0.001$, $F_{1, 119} = 0.001$, $P = 0.972$). Age classes are not significantly different for head shape ($R^2 = 0.024$, $F_{1, 119} = 1.475$, $P = 0.115$), but were for size ($R^2 = 0.061$, $F_{1, 119} = 3.828$, $P = 0.023$). Head size does not vary much between males and females within age classes, but does between them (Fig. 3). In the
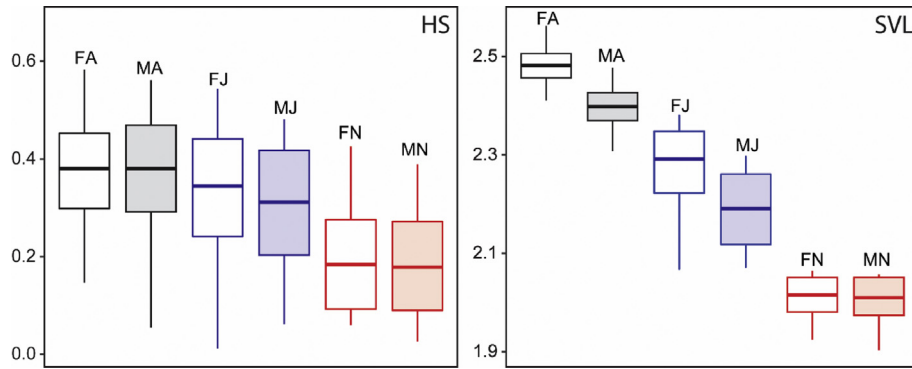
Fig. 3. Boxplot representing variation in head size (left) and SVL (right) of *Atractus reticulatus* males and females during different ontogenetic stages. F = Females; M = Males; A = Adults; J = Juvenile; N = Neonate.
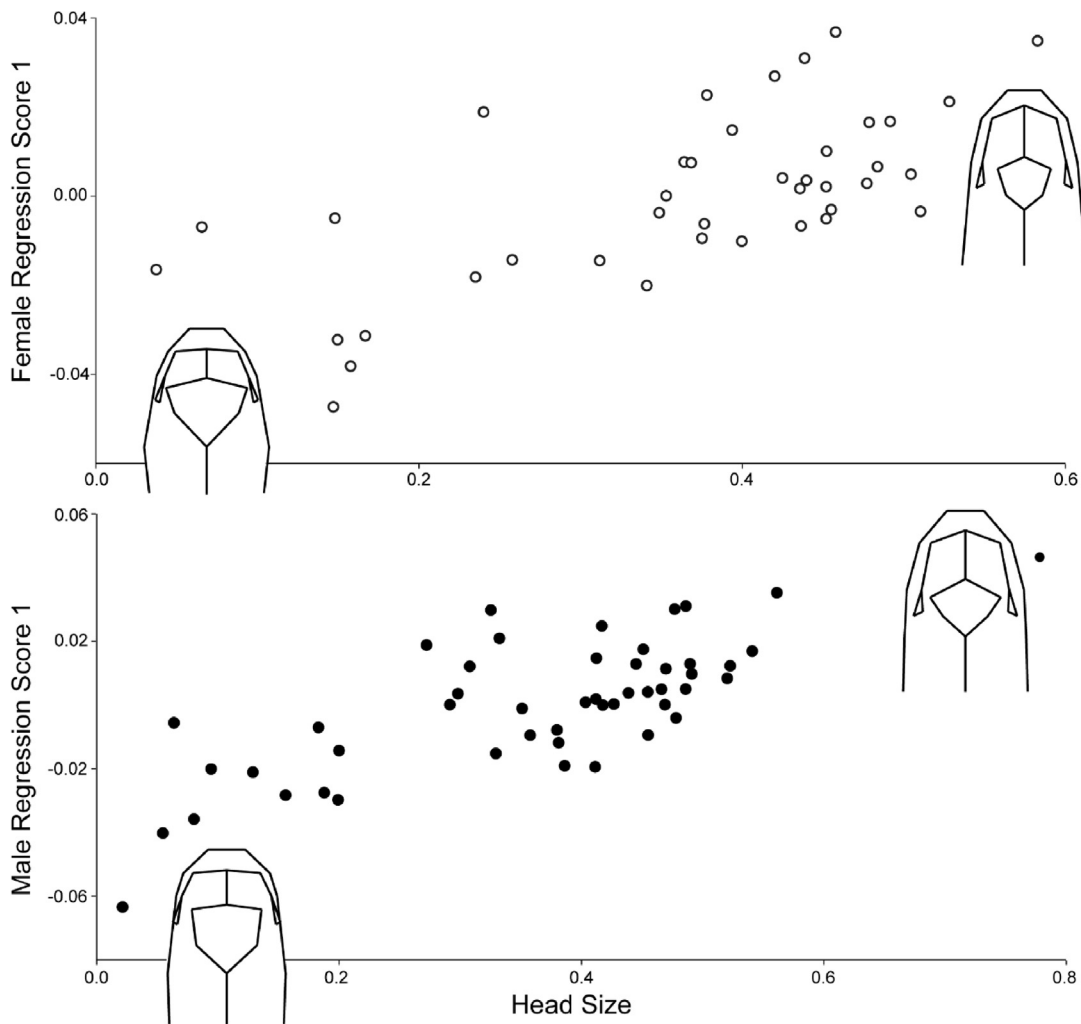

Fig. 4. Effect of head size on adult female (above) and male (bellow) head shape variation of *Atractus reticulatus*.

case of SVL, variation between female and male increases as the age class increases varying from showing almost no differences in sexual dimorphism as neonates and to high degree of sexual dimorphism as adults (Fig. 3). The calculated values of sexual dimorphism support this as the mean values of sexual dimorphism increase from neonates to adults in SVL, but not for head size and shape (Table 2).

Female allometry was significant (4.86%, $P = 0.008$), while in males was not (1.70%, $P = 0.394$). Females show a more linear pattern of growth than males. In summary, female head shape in neonates to smaller juveniles tend to be more squared, with proportionally larger and squared prefrontal shields and wider, but shorter frontal shields. Orbital opening is longer and thinner (Fig. 5). In males, neonates and smaller juveniles tend to be more

Table 2
Mean sexual dimorphism calculated values for head shape (HSh), size (HS) and snout-vent length (SVL), separated by age classes.

	HSh	HS	SVL
Neonate	0.0656	0.0138	0.0070
Juvenile	0.0216	0.0195	0.0879
Adult	0.0425	0.0008	0.0954

triangular head, with proportionally larger prefrontal shields and wider and shorter frontal shields. Orbital opening is longer and thinner (Fig. 5).

Regression between SVL and HS is significant in both sexes (Females: Adj $R^2 = 0.060$, $F_{1, 57} = 4.724$, $P = 0.034$; Males: Adj $R^2 = 0.053$, $F_{1, 59} = 4.364$, $P = 0.041$). Trend shows that SVL and HS tend to increase together, however, the plot also shows a large portion of unexplained residuals in both sexes, that is, head size often overlaps between age classes (Fig. 6).

4. Discussion

We found significant differences in head shape and SVL between males and females of *A. reticulatus*, but not in head size. Although the head shape overlaps between sexes is extensive, our results show that adult males can present proportionally slender heads than females at the extreme of their morphospace variation, reflecting in the prefrontals (wider and more elongated) and frontal (wider) shape of the males. Regarding head size, previous studies
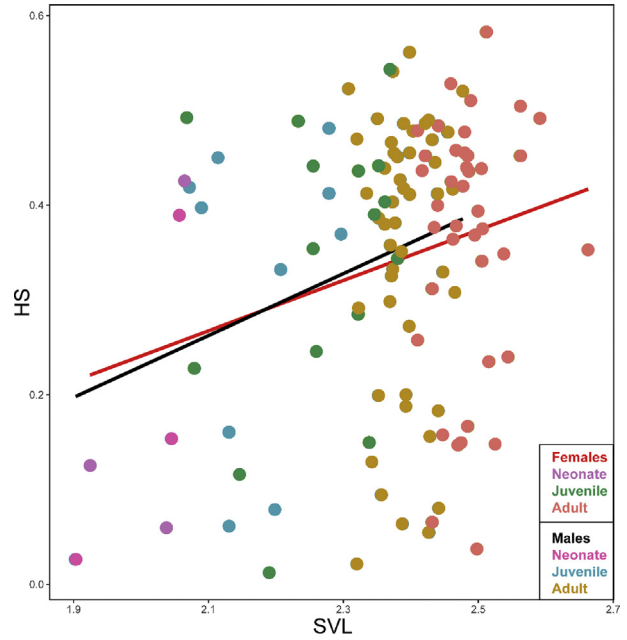

Fig. 6. Linear regression plot of the SVL vs. HS of female and male ontogenetic samples in *Atractus reticulatus*. Different sexes and age classes are coloured as in the legend embed in the plot. Coloured figure only available in the online version of this manuscript.
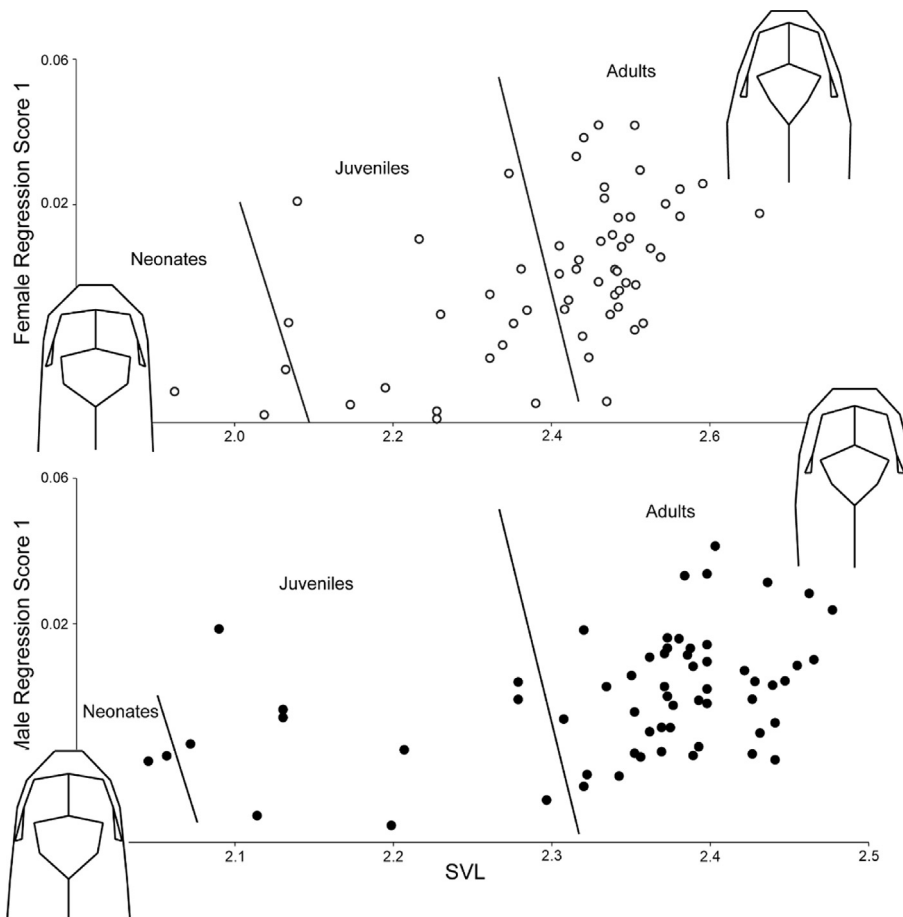

Fig. 5. Effect of SVL on head shape variation of female (above) and male (bellow) ontogenetic samples of *Atractus reticulatus*.

on non-fossorial snakes have found clear sexual dimorphism in this trait (Shine & Crews 1988; Camilleri & Shine 1990; Silva et al. 2017; Tamagnini et al. 2018; Loebens et al. 2019; Murta-Fonseca et al. 2019). We hypothesize that, because *A. reticulatus* is a semifossorial species, it does not support that much difference of head size between sexes in order to perform digging function (Savitzky 1983). On the other hand, such a constraint may be also the reflection of a homogeneous diet based on earthworms throughout its development (Passos et al. 2019). Indeed, species with secretive lifestyles such as *Atractus* usually have a slender and longer head regarding species presenting other habits (Cundall & Irish, 2008). In fact, similar pattern has been found to other species of cryptozoic habits and diets composed of elongated prey (Braz et al. 2019).

Males and females of *A. reticulatus* differ in head shape. Since sexual dimorphism in the head shape does not appear to be guided by sexual selection in snakes, usually such difference are related to the consumption of different prey types or sizes (Camilleri & Shine, 1990). Despite the few existing dietary studies of *Atractus* species, the prey spectrum explored by these snakes appears to be reduced to elongated body invertebrates (Passos et al., 2019). *A. reticulatus* is no exception, displaying a specialized earthworm diet, especially from the family Megascolecidae (Balestrin et al., 2007). Therefore, if there is any difference in diet between males and females of *A. reticulatus*, it can only be a response to the ingestion of earthworms of different sizes. A similar case has been observed for the rattlesnake *Crotalus polystictus* (Cope, 1865), a species in which males have more robust heads than females and eventually consume larger prey (Meik et al., 2012). Another relevant issue is that the largest species of the genus *Atractus* (adults > 1000 mm SVL) differ in their feeding apparatus, such as the elongation of the gnathic complex and the rotation of the quadrate, characteristic of snakes able to consume large prey (Cundall & Greene, 2000; Scanferla, 2016; Passos et al., 2019). Even though *A. reticulatus* is not a large species (males < 280 mm, females < 390 mm SVL), sexual dimorphism in SVL and head shape may suggest prenatal differences in ossification timing of the feeding apparatus between the sexes (Lees et al., 2012). Additionally, some studies have postulated that snakes with proportionately short and robust heads make stronger bites, a feature that has probably evolved to assist prey control and swallow (Mori & Vincent 2008; Andjelković et al. 2016; Tamagnini et al. 2018). If the more robust heads of *A. reticulatus* females also reflect stronger bite force, this may enable them to overcome and consume larger and stronger earthworms; consequently, they could exploit an inaccessible niche for most males of the same species. Although we concede that these hypotheses are speculative, they can be useful for understanding how natural selection acts to reduce resource competition between sexes.

We have detected both static and ontogenetic allometry in our sample. However, there are clear differences between sexes towards these results. As a rule, males of *A. reticulatus* have stronger static allometry than females, while females have ontogenetic association between head shape in interaction with SVL. This is a direct effect of the different variables used to analyse the selection of head shape traits in each dataset. In static allometry, adult males and females differ in the percentage of HSh that is associated with HS, but the general traits associated with the increase of HS are the same for both sexes. Adult males are more strongly affected than females in this dataset and this possibly related to the largest variation in head size within this sex. Similar patterns have been reported for other animal groups (Astúa et al. 2000; Astúa 2015). However, why head size is more variable in males than in adult females of *A. reticulatus* is an open question—even though it is widely known that activity pattern of males is more intense during the reproductive season (reviewed in Whitfield & Semlitsch 1987), influencing several key life history parameters, such as

physiological condition and fitness (Lourdais et al. 2014). In parallel, some morphological traits play an important role for macrohabitat selection and substrate use (Lawing et al. 2012). So, the head lability could be related to more general aspects of male's spatial ecology. On the other hand, Tamagini et al. (2018) speculated that the higher percentage of explanation of head shape variation in males of *V. berus* may be the result of sexual selection, in a context in which larger heads could help during male–male combats or represent some signal to competing males.

Male–male combats are distributed across different snake lineages and are related to the largest increase in male SVL, but there is no convincing evidence that head size or shape plays an important role in this matter on taxa without a significantly different SSD (Shine 1978; Rivas & Burghardt 2001; Senter et al. 2014). In fact, there is no record of male–male combat in *A. reticulatus* (Balestrin & Di-Bernardo, 2005) or for any other congener. In addition, male–male combat behavior was probably not present in the most recent exclusive common ancestor to Dipsadidae snakes, since among the more than 800 species within this family such behavior was only recorded in *Imantodes cenchoa* (Linnaeus, 1758), in which it probably evolved independently (Pizzatto et al., 2008; Senter et al., 2014). However, due to the lack of natural history data, especially concerning reproductive behavior in *Atractus* species, we cannot currently infer whether male head size and shape is related with male–male combat suitability.

The congruence of male and female shape deformations associated to HS increase of *A. reticulatus* fits in the hypothesis that closely related taxa tend to have less divergence in their allometric slopes (Voje et al., 2013). Moreover, the allometric transformation of the cephalic shields is congruent with the constrain for semifossorial lifestyle with narrowing and elongation of the braincase (Cundall & Irish 2008). In *A. reticulatus*, males and females do not appear to differ in behavior, activity pattern or habitat use, probably always foraging at twilight or at night and on the ground (Balestrin et al., 2007), which probably justifies our result.

The ontogenetic allometry (measured with SVL) found for females, but not for males, may be due to the simple fact that females can reach higher SVL variation than males, presenting greater ontogenetic variation, reaching maturity later than males (Balestrin & Di-Bernardo 2005), a putative heterochronic post-displacement effect (cf. Rivas & Burghardt 2001). For example, Murta-Fonseca & Fernandes (2016) demonstrated significant ontogenetic allometry, with head size, in the skull of *Hydrodynates gigas*, a large (~2.5 m) semi-aquatic snake that also exhibits large ontogenetic variation of SVL. In contrast with Murta-Fonseca & Fernandes (2016), in our dataset HS is much more variable within age classes, that is, juvenile and adult specimens often have similar head size, so HS and SVL do not proportionally grow in *Atractus reticualtus*—although a linear, but weak trend between HS and SVL is detectable in both sexes (our results, Fig. 6). In fact, we have regressed HS in the ontogenetic sample and the pattern holds the same as the one encountered for static allometry procedure (results not shown). In summary, this shows that the traits of head shape that are selected by the increase of SVL are not necessarily the same that are selected by HS.

Although there is an ontogenetic allometric effect on the head shape of females (but not on males), when associated to SVL, female neonates and smaller juveniles tend to have squared heads, while in males of the same categories the heads tend to be more triangular. This result—that males and females may be sexually dimorphic in head dimensions from the earliest stages of life—is consistent with other studies and reinforce that certain morphological traits begin to distinguish before birth (Shine & Crews 1988; King et al. 1999; but see Tomović et al. 2010; Silva et al. 2017). On the other hand, differences in SVL in neonates are practically

unnoticeable, but increase dramatically in juveniles and reach the highest levels in adults (Table 2, this study). The same results were found by a large number of authors for different snake groups and may be explained by differences in growth trajectories between the sexes (e.g., Beaupre et al. 1998; Shine 1994; Tomović et al. 2010; Stuginski et al. 2017).

The female-biased SVL corresponds to the most common pattern in snakes. It probably evolved through fecundity selection (Shine 1978; Gregory 2004). Usually the size of offspring is female-size dependent, and larger litters are more likely to survive (Ford & Seigel 1989; Shine 1994). Traditionally, this pattern has been explained through two distinct mechanisms: (1) a delay in female maturation, which gives females more time to convert energy into growth before reproduction (Madsen 1983; Baron et al. 2010); and (2) higher growth rates in females, guided by more food consumption (Pearson et al. 2002; Stuginski et al. 2017) or different thermoregulatory strategies compared to males (Gregory et al. 1999; Tanaka 2007, 2008; Harvey & Weatherhead 2010). Congruent to the delayed maturation mechanism in females, Balestrin & Di-Bernardo (2005) suggested that in *A. reticulatus* males reach sexual maturity between 8 and 10 months old (~198 mm SVL), while females reach 11−12 months old (~242 mm SVL). This fits with our results in the context that we found most of the variation to be explained by sexual dimorphism in the adult sample (52%) than in the immature individuals (5%). However, this does not exclude the possibility that there are other mechanisms underlying these differences. For example, that females may grow faster than males in the first months of life or maintain high growth rates even after sexual maturity (Webb et al. 2002; Aubret & Shine 2007; Stuginski et al. 2017).

In this study, we identified significant differences between male and female of *A. reticulatus* in body size (larger in females) and head shape (females with proportionally more robust heads), but not in head size. More precisely, males and females are sexually dimorphic in head shape even in neonates, indicating that this differentiation is prenatal. More robust female heads may be associated with trophic segregation, enabling them to ingest larger prey than males. Contrary to head shape, SVL dimorphism progressively increases over ontogeny, which is possibly related to the late sexual maturation of females and/or different growth rates between the sexes. Adult males have higher allometric strength than females, while females have association between head shape and body length, but males do not. The higher allometric strength in males may underlie some unknown mechanism of male competition or selection by females, while ontogenetic allometry of females probably evolved from fecundity selection. Finally, we find that the direction of the allometric slopes is convergent in *A. reticulatus*, a result that fits the expected for sexes exploring similar environments. The morphological differences we find in this study will be better understood once physiological and natural history gaps are filled for this species.

Declaration of competing interest

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jcz.2020.05.008.

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