



Research Paper

Sexual dimorphism and ontogenetic changes of Amazonian pit vipers (*Bothrops atrox*)



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ABSTRACT

Sexual dimorphism of body size (SSD) is widespread in snakes and has been the subject of numerous studies, but few have examined sexual shape dimorphism (SShD). The present study explores sexual size and shape dimorphism in the Amazonian pit viper *Bothrops atrox*. We combine linear and geometric morphometrics to describe differences in body size and head shape between the sexes and how these differences are generated throughout ontogeny. Our study shows that *B. atrox* is sexually dimorphic, with females being larger than males, except for tail length. Females also have relatively larger heads, differing not only in size but also in shape. Our results reveal that both size and shape of the head vary significantly from neonates to adults. Head shape changes in *B. atrox* are associated with allometry and follow similar trends in both sexes: neonates have a relatively shorter and more robust head and shorter snout, while adults show a wider and flattened head. Although our results indicate that allometry is an important factor in determining sexual shape dimorphism, additional studies on diet and performance may be necessary to understand the ecological implications of such differences.

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1. Introduction

Sexual dimorphism is a widespread phenomenon among many groups of animals and may be expressed by differences in physiology, behavior or ecology between males and females within species (Butler et al., 2000; Vincent et al., 2004a; Gidaszewski et al., 2009; Herler et al., 2010; Sanger et al., 2013). Many vertebrate studies have analyzed such divergence in traits between males and females, as well between adults and juveniles, often associated with adaptive differences or ecological consequences (Cox et al., 2003; Gregory, 2004; Vincent et al., 2004b; Mitteroecker et al., 2013). Different factors that might influence differences between adults of different sexes include size at birth, duration and rate of growth,

survival, and timing of sexual maturity (Shine, 1990; Haanel and John-Alder, 2002).

Different mechanisms that drive the evolution of sexual dimorphism have been proposed: (1) ecological selection – niche partitioning via prey divergence (Shine, 1989; Vincent et al., 2004a); (2) fecundity selection – when larger females have larger clutches compared to smaller females (Griffith, 1990; Kuo et al., 2009); and (3) sexual selection – when larger males are more successful in male–male combats to gain access to mating or are more attractive to females (Shine, 1994, 2000; Bovero et al., 2003). Sexual differences can result in sexually divergent growth trajectories, in which one sex grows faster than the other with both sexes reaching sexual maturity at the same age, or when both sexes grow at the same rate, but one sex reaches sexual maturity at a relatively older age (Andrews, 1982; Parker and Plummer, 1987; Kozłowski, 1989).

Most studies on the evolution of sexual dimorphism refer to size dimorphism (SSD), which occurs when individuals of one sex are characteristically larger than those of the opposite sex for a given

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population or species (Cox et al., 2006). Recently, shape analysis has been considered as the most efficient and complete method for quantifying sexual dimorphism, because different parts of the body part serve different functions even where size and shape are related to one another (Kaliontzopoulou et al., 2008). However, sexual shape dimorphism (SShD) has been much less investigated than sexual size dimorphism (Gidaszewski et al., 2009). Sex distinctness in body shape can be expressed as differences in body proportions, and in skull shape in numerous taxa, including fish, amphibians, birds, turtles, lizards, and snakes (Vincent et al., 2004a; Butler et al., 2007; Berns and Adams, 2010; Herler et al., 2010; Ceballos and Valenzuela, 2011; Sanger et al., 2013; Zhang et al., 2014).

In reptiles, sexual dimorphism may result from factors operating prior to maturity (e.g. Shine, 1990; Cox et al., 2007; Kaliontzopoulou et al., 2008; Ceballos and Valenzuela, 2011). The direction and degree of SSD attained before maturity is typically highly correlated with the degree of SSD at mean adult size. Thus, when SSD appears in juveniles, it is very likely to be reflected in adult body sizes (Shine, 1990). In addition to sexually dimorphic growth rate, some authors suggest that SSD may be caused by other factors including neonatal size, growth duration, maturity, and survival (Trivers, 1976; Stamps, 1983, 1993; Andrews and Stamps, 1994; Haenel and Johan-Alder, 2002).

Sexual size dimorphism in snakes is generally well documented (e.g. Solórzano and Cerdas, 1989; Rivas and Burghardt, 2001; Krause et al., 2003; Furtado et al., 2006; Pinto et al., 2008), however, sexual shape dimorphism has been poorly studied (Gregory, 2004; Vincent et al., 2004a, 2004b; Smith and Collyer, 2008; Tomovic et al., 2010). In most snakes, females reach larger sizes than males reversing the typical pattern of terrestrial vertebrates where males have equivalent or larger sizes than females (Shine, 1994). Beyond differences between the sexes, snakes can show a variety of changes during their lifetime. Juvenile and adult snakes show differences in body size and other behavioral, morphological, and physiological characteristics that may lead to an ontogenetic shift in diet, coloration, foraging behavior, habitat use, and venom composition (Mushinsky et al., 1982; Mushinsky, 1987; Sazima, 1991; Lind and Welsh, 1994; Vincent et al., 2004a,b, 2006; Zelanis et al., 2007).

Snakes of the genus *Bothrops* Wagler, 1824 comprise about 50 species, have a large radiation in the Neotropical region, occurring from Mexico to Argentina (Barbo et al., 2016). These species occupy several environments with many types of microhabitats. Therefore, they vary in body shape, use of the environment as well as in eating habits (Parkinson, 1999; Martins et al., 2001, 2002; Campbell and Lamar, 1989). Although sexual dimorphism and ontogenetic changes in diet and substrate have already been documented for some species of *Bothrops* (Cunha and Nascimento, 1975, 1978; Dixon and Soini, 1986; Oliveira and Martins, 2001; Turci et al., 2009), there is no study exploring in greater detail if these differences also occur in the head shape and body between the sexes and age groups. Among species of *Bothrops*, *B. atrox* (Linnaeus, 1758) is the most widely distributed throughout the northern region of South America, including the Brazilian Amazon (Cunha and Nascimento, 1978; Wüster et al., 1996; Carrasco et al., 2012). It is primarily nocturnal, although diurnal activity is not uncommon (see also Egler et al., 1996). It has a generalist diet, preying on invertebrates (e.g. centipedes) and vertebrates (e.g. fish, amphibians, lizards, other snakes, birds and small mammals) (Oliveira and Martins, 2003; Turci et al., 2009; Fraga et al., 2013; Rodrigues et al., 2016). Several studies on the biology of *B. atrox* have shown that juveniles are arboreal and feed on ectothermic prey while adults are terrestrial and feed on endothermic prey (Henderson et al., 1976, 1979; Zimmerman and Rodrigues, 1990; Oliveira and Martins, 2001).

Here we explore sexual size and shape dimorphism in the Amazonian pit viper *Bothrops atrox*. We combine linear and geometric

morphometrics to explore and describe differences between sexes and age classes regarding body size and head shape to understand sexual and ontogenetic shifts. We examine absolute sexual differences in head and body dimensions and geometric head shape in adults, juveniles and neonates to gain insights into the starting and ending points of ontogenesis in males and females. We focus on head shape development and investigate how head dimensions vary with head size, aiming to detect specific head features that might exhibit an over-development in one sex independent of total head size as well as to detect those features that are particularly modified during ontogeny. We address the following points: (1) is sexual size dimorphism followed by shape sexual dimorphism of the body and the head? (2) what is the pattern of variation in head and body shape between male and female? (3) does ontogenetic allometry vary between sexes and, if they do, are they enough to explain sexual dimorphism? and (4) what is the moment in development at which changes in the shape of the head of males and females occur, if they exist?

2. Materials and methods

2.1. Specimens and data collection

We analyzed a total of 198 preserved specimens (111 males and 87 females) of *Bothrops atrox* from different populations of the Amazon, housed in the herpetological collection “Oswaldo Cunha” of the Museu Paraense Emílio Goeldi (MPEG), in the municipality of Belém, state of Pará, Brazil (Appendix A). We verified the sex of each specimen through an incision in the first subcaudal scales. The age group of individuals followed the categories described in the literature, considering: neonate males and females with umbilical scar (SVL below 300 mm); immature juvenile males (SVL between 300 and 460 mm) and immature juvenile females (SVL between 300 and 800 mm); mature adult males (SVL above 470 mm) and mature adult females (SVL above 850 mm) (see Hoge and Federsoni, 1976/77; Cunha and Nascimento, 1982; Oliveira and Martins, 2001; Oliveira, 2003).

2.2. Linear morphometrics and statistical analyses

To test differences in head and body size, we measured the following morphological features: snout-vent length (SVL), from the tip of the snout to the cloaca; tail length (TL), from the cloaca to the end of the tail; head length (HL), from the tip of the snout to the quadrate-mandibular articulation; head width (HW), measured at the widest part; distance between the eyes (DE), measured as the maximum distance between the internal border of the orbits, in the preocular scale; and maximum distance between the nostrils (DN). Measurements were taken using a digital caliper with 0.01 mm precision for structures smaller than 120 mm, and a tape measure with 1 mm precision for structures larger than 120 mm.

To investigate the multivariate patterns of variation between sexes and age classes we performed a Principal Component Analysis on the log-transformed linear variables. Differences between sexes was tested for neonates and adults through a Multivariate Analysis of Variance (MANOVA). To quantify groups multivariate superposition, we performed a Linear Discriminant Analysis (LDA) using the interaction between age and sex as a factor and used the correct reclassification rates of the LDA as a measure of group superposition in the multivariate space (Santos et al., 2017). Because the juvenile class was morphologically more variable than neonates and adults, they were excluded from the training set. Thus, the LD functions were calculated first only neonates and adults, and then scores on those functions were calculated *a posteriori* for the entire sample, including juveniles.

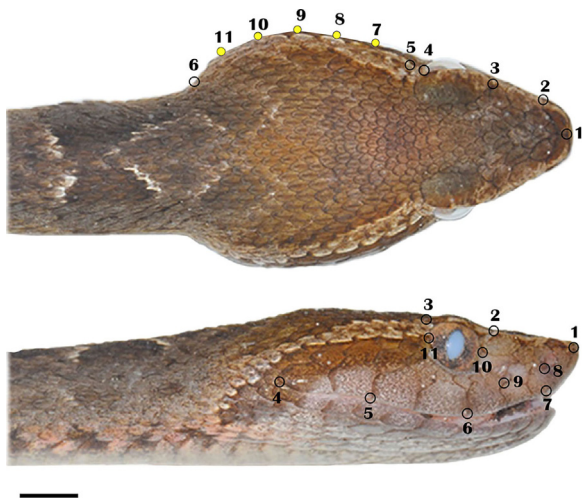


Fig. 1. Landmarks used for the head shape analysis of *Bothrops atrox*. (A) Dorsal view: 1- intersection of internasal scales; 2- intersection of internasal and cantal scales; 3- intersection of cantal and supraocular scales; 4- intersection of supraocular and postocular scales; 5- end of 1st postocular scale; 6- head-neck inflexion point; 7–11- equidistant semilandmarks at the head contour. (B) Lateral view: 1- intersection of rostral, internasal and prenasal scales; 2- intersection of supraocular and preocular scales; 3- intersection of supraocular and postocular scales; 4- end of the 7th supralabial scale; 5- intersection of 5th and 6th supralabials scales; 6- intersection of 3rd and 4th supralabials scales; 7- intersection of 1st supralabial and rostral scales; 8- intersection of nasals scales; 9- intersection of loreal and 2nd supralabial scales; 10- intersection of preoculars scales; 11- intersection of postoculars scales. Scale bar: 10 mm.

To evaluate how observed patterns of sexual dimorphism were generated throughout ontogeny we performed a cubic polynomial regression between each variable and SVL. To test if ontogenetic allometry differed between sexes we performed an analysis of covariance (ANCOVA) between sexes including interaction terms. This allowed us to quantify if the polynomial terms of the regression differed between sexes. To reduce over-parameterization, we produced simpler models by removing non-significant terms in a stepwise manner, from higher order to lower order terms, starting with interactions. At each step, the reduced model was compared to the full model through a likelihood ratio test using a χ -square distribution. The process stopped when the removal of any term from the model resulted in a model what was significantly different from the full model.

2.3. Digitalization of landmarks and shape analyses

For Geometric Morphometrics (GM) we analyzed a total of 94 individuals of *Bothrops atrox* (females = 46; males = 48). Specimens were photographed using a digital SLR camera (Nikon D90) coupled to a 105 mm macro lens on a tripod. Each image included a scale, and landmarks were digitized using tpsDig2 v.2.18 (Rohlf, 2015). To quantify head shape and size, a total of 22 landmarks were digitized on dorsal and lateral views of the specimens. Eleven of these represent the dorsal view with six fixed anatomical points and five equidistant semilandmarks that captured the contour of the head; and eleven landmarks represent the lateral view of the head (Fig. 1). Landmarks were ontogenetically stable, such that they could be located from neonates to adults. To avoid redundant information in symmetric structures we digitized landmarks only on the left side.

To extract geometric shape information, landmark configurations were subjected to a Generalized Procrustes Analysis (GPA) (Rohlf and Slice, 1990) to remove effects of location, orientation, and scale, the residuals of which were used as shape variables in all analyses (Rohlf and Slice, 1990; Zelditch et al., 2004). Semiland-

Table 1

Loadings of each trait on the axes of the Principal Component Analysis (PCA) and the percentage explained by each one. Abbreviations: SVL, snout-vent length; TL, tail length; HL, head length; HW head width; DE, distance between eyes; DN, distance between nostrils; %var, variance explained for each axis.

Variables	PC1	PC2	PC3	PC4	PC5	PC6
SVL	-0.494	0.217	-0.084	0.168	0.701	-0.427
TL	-0.496	0.607	0.434	0.075	-0.410	0.153
HL	-0.376	-0.185	-0.238	0.074	0.255	0.835
HW	-0.366	-0.397	-0.310	0.578	-0.464	-0.251
DE	-0.326	0.089	-0.555	-0.704	-0.245	-0.148
DN	-0.359	-0.620	0.586	-0.362	0.030	-0.109
%var	96.28	1.54	1.11	0.52	0.32	0.23

Table 2

MANOVA of log-linear measurements for the difference between sexes for neonates and for adults specimens. Df- degrees of freedom; Wilks- Wilks' Lambda; num Df- Numerator degrees of freedom; den Df- Denominator degrees of freedom; approx F- Approximated F statistic; R²- Coefficient of determination; p- probability of the null hypothesis given the data. Bold values were considered statistically significant (p < 0.05).

	Df	Wilks	approx F	num Df	den Df	R ²	p
Neonates							
sex	1	0.710	2.445	6.000	36.000	0.560	0.044
residuals	41						
Adults							
sex	1	0.309	24.969	6.000	67.000	0.468	0.000
residuals	72						

marks positions were optimized according to Procrustes Distance criteria. Head size was calculated as centroid size (CS), which is the square root of the summed squared distances between the centroid and each anatomical landmark of a given configuration (Zelditch et al., 2012).

Patterns of multivariate difference were investigated using PCA and LDA approach described above for linear variables, with shape variables as predictors of group (sex and age classes, excluding juveniles) membership in the case of LDA. To reduce incorrect group discrimination caused by low signal-to-noise ratio (Strauss, 2010; Mitteroecker and Bookstein, 2011), we used only PCs summarizing 95% of the variation on the LDA. To test differences between sexes for neonates and adults, we employed a non-parametric Procrustes ANOVA approach (Klingenberg, 1998) in which differences are tested through multivariate linear models and significance is accessed through permutations.

The ontogeny of shape sexual dimorphism was evaluated through multivariate allometry analysis following the non-parametric approach used by Collyer et al. (2015). This approach consists of investigating the multivariate differences between sexes using size (logCS) as a covariate. The presence of a significant interaction term between sex and size means that sexes are different in the regression coefficients, thus differing in their ontogenetic allometry. In order to visualize the relationship between size and shape, regression scores were calculated as the shape changes that were mostly aligned with variation in size (Drake and Klingenberg, 2008).

All tests were performed in the Geomorph package v.2.1.5 of R (Adams and Otárola-Castillo, 2013). Significance of non-parametric tests was accessed through 10.000 permutations.

3. Results

3.1. Linear morphometrics

The first two axes of the PCA summarize 97.83% of the total between-group variation. The first axis has negative loadings on all variables and represents a general size dimension (Table 1) and

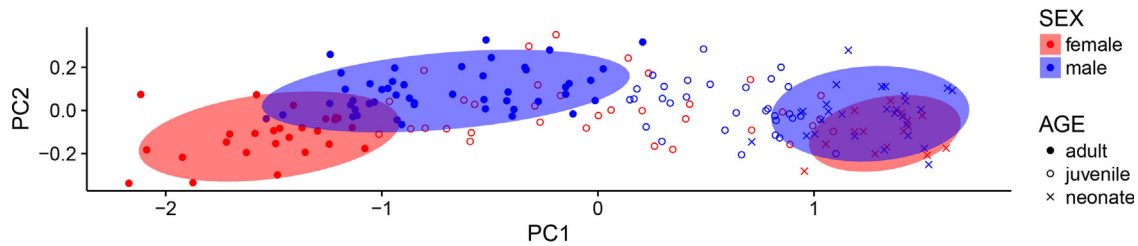


Fig. 2. First two axes of Principal Component Analysis over the log-transformed linear morphometric variables of *Bothrops atrox*. Ellipses represent only neonates and adults.

Table 3

Procrustes ANOVA for the shape difference between sexes for neonates and for adult specimens. Df- degrees of freedom. SS- sum of squares. MS- Mean Squares. R²- Coefficient of determination. F- F statistic. p- probability of the null hypothesis given the data. Bold values were considered statistically significant ($p < 0.05$).

		Df	SS	MS	R ²	F	p
Dorsal view	<i>Neonates</i>						
	sex	1	0.002	0.002	0.064	1.771	0.122
	residuals	26	0.027	0.001			
	total	27	0.029				
	<i>Adults</i>						
	sex	1	0.01	0.01	0.208	8.923	0.001
residuals	34	0.036	0.001				
total	35	0.046					
Lateral view	<i>Neonates</i>						
	sex	1	0.006	0.006	0.104	3.012	0.002
	residuals	26	0.051	0.002			
	total	27	0.057				
	<i>Adults</i>						
	sex	1	0.019	0.019	0.167	6.801	0.001
residuals	34	0.093	0.003				
total	35	0.112					

Table 4

Multivariate Regression between shape and size using sex as a factor. Df- degrees of freedom. SS- sum of squares. MS- Mean Squares. R²- Coefficient of determination. F- F statistic. p- probability of the null hypothesis given the data. Bold values were considered statistically significant ($p < 0.05$).

	Df	SS	MS	R ²	F	p	
Dorsal view	log(size)	1	0.078	0.078	0.449	76.875	0.001
	sex	1	0.003	0.003	0.019	3.309	0.008
	residuals	91	0.093	0.001			
	total	93	0.175				
Lateral view	log(size)	1	0.138	0.138	0.379	58.507	0.001
	sex	1	0.012	0.012	0.032	4.958	0.001
	residuals	91	0.214	0.002			
	total	93	0.363				

mainly distinguishes between neonates and adults (Fig. 2). The second axis represents a contrast between adult males having longer tails and smaller heads than adult females, which have smaller tails and larger heads (Table 1). The MANOVA scores between sexes were marginally significant for neonates (Table 2), showing moderate superposition on the multivariate space (83.72% correct LD classification rate). For adults, differences were more evident, with MANOVA being highly significant (Table 2) and with sexes showing almost no morphospace superposition (94.60% correct classification rate).

Full regression models between TL, HL and HW showed a significant effect of sex, a fact that is consistent with the presence of sexual dimorphism in these variables when we account for differences in size (SVL, Table S1). Despite that, with the exception of DN, no regression showed a significant interaction between the linear or higher order terms with sex. Furthermore, when we produced reduced models no interaction term was kept (Table S1), suggesting that allometric relationships are the same between sexes and stay that way throughout ontogeny. Specifically, males show higher values of TL from birth and keep that trait until adulthood, being surpassed in tail length only due to the fact that females grow to larger sizes (Fig. 3). Females, on the other hand, are already born with larger heads, both in length (HL) and width (HW), and keep larger heads also by growing to larger sizes (Fig. 3). Except for DE, all the chosen polynomial regressions included higher order terms (quadratic or cubic), showing that the allometric relation between variables and SVL changes along the ontogeny (Fig. 3; Table S1).

3.2. Geometric morphometrics

The Principal Component Analyses (PCA) of shape variables shows that the first seven and twelve Principal Components explains approximately 95% of variation for dorsal and lateral

views, respectively, and were thus retained for the LDA (Fig. 4A,B). The first two PCs axes for analysis of the dorsal and lateral views of the head explained 73.03% and 58.31% of the variance, respectively (Fig. 4C,D). The multivariate ordination on the two first PCs showed a similar pattern in dorsal and lateral views (Fig. 4), with the first axis discriminating between neonates (larger values) and adults (smaller values). Furthermore, both male and female neonates show a large superposition on both PC1 and PC2, while adult specimens are less superimposed.

The Procrustes ANOVA results for the dorsal view was not significant for the distinction between sexes in neonates (Table 3). For adults, sexes showed significant differences in the dorsal view (Table 3) and less morphospace overlap than that observed in neonates (60.71% of correct LD classification rate for neonates and 86.11% of correct LD classification rate for adults). For the lateral view, both neonates and adults showed a significant sexual dimorphism in the Procrustes ANOVA (Table 3), with no evident decrease in morphospace overlap between groups (neonate correct LD classification = 85.71%; adult correct LD classification = 88.89%).

The multivariate regression analysis using both logCS and sex as factors shows that, for the dorsal view, allometry accounted for 48.91% of total shape variance, while for the lateral view, allometry accounted for 37.88% of total shape variance. Tests of homogeneity of slopes failed to show any significant difference of slopes between sexes (significance of a test for the interaction term was $p = 0.196$ and $p = 0.336$ for dorsal and lateral views, respectively), suggesting that shape allometry is similar among sexes. Regression scores for both views suggest that sex differences are partly due to the fact that females are larger and also present more robust head shapes (Fig. 5). Multivariate regression shows that sex differences are significant, even after accounting for allometric differences, despite the fact that size-free sex differences account for very little of the total shape variation (Table 4). The axis representing allometric variation is nearly identical to the PC1 axis for both dorsal (vector correlation = 0.995) and lateral (vector correlation = 0.982) views.

Based on the deformation grids, size-dependent shape changes in dorsal view are expressed as elongating and widening of the head. Neonates have a smaller and narrower head than

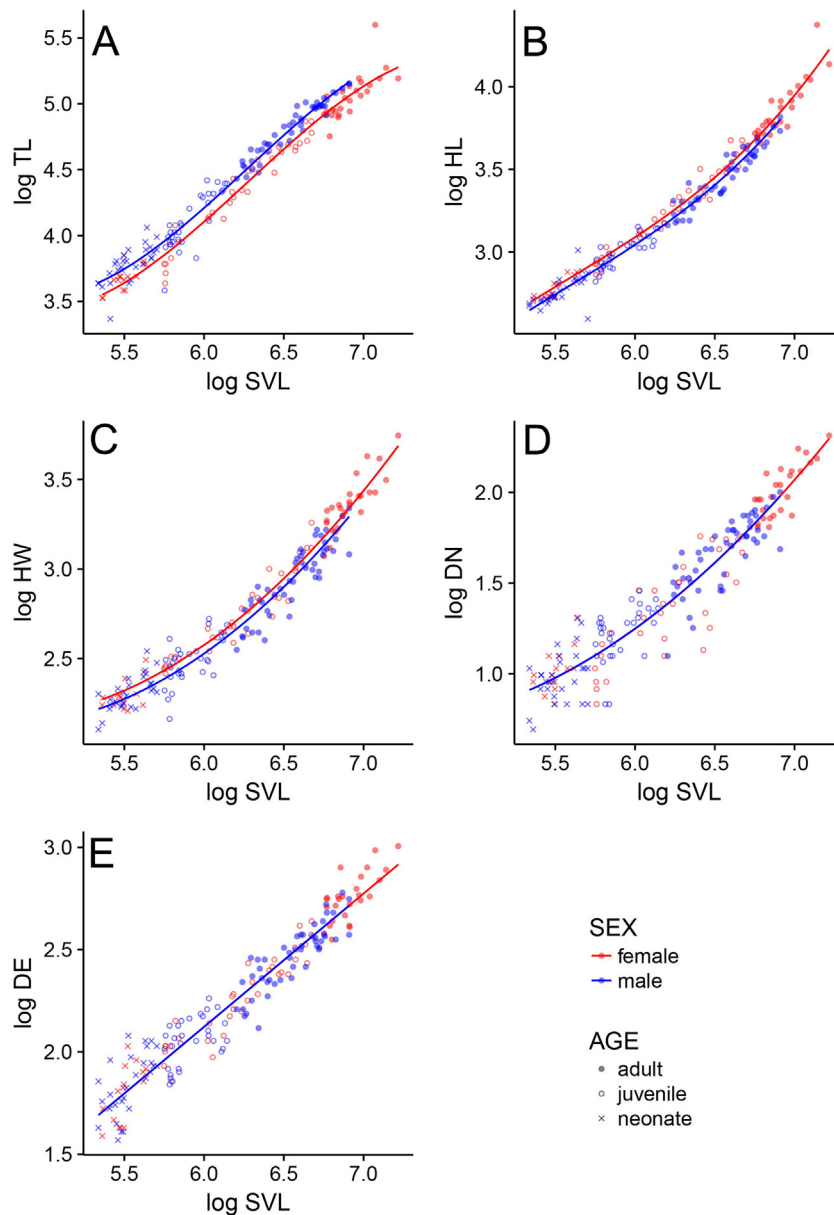


Fig. 3. Relationship of tail length (A), head length (B), head width (C), distance between nostrils (D), and distance between eyes (E) with snout-vent length in males and females of *Bothrops atrox*.

adults. Juveniles and adults show an enlargement in the posterior region of the head, which becomes wider in females than males (Fig. 5A). Changes in the lateral view shows neonates with a more pronounced snout, proportionally larger eyes and higher head, becoming more flattened in adults with proportionally smaller eyes (Fig. 5B).

4. Discussion

This study has demonstrated that *Bothrops atrox* shows not only significant sexual dimorphism in body size (females larger), tail size (longer in males) and head dimensions (females with longer and wider heads; Figs. 2 and 3), but also in head shape (Fig. 4). Head shape variation between sexes was largely consistent with allometric scaling, with females having morphologies that are more robust and associated with larger heads (Fig. 5). Sex differences were present even after controlling for differences in size, but these differences explained very little of the shape variation

(Table 4). In addition to sexual dimorphism, we also found that head shape varied between ages, with shape changes being produced via ontogenetic allometry. The marked sexual size dimorphism (SSD) observed in *B. atrox* is consistent with earlier studies and have been reported for other species of *Bothrops*, where females reach greater body length than males (e.g. Sazima and Manzani, 1998; Valdujo et al., 2002; Nogueira et al., 2003; Hartmann et al., 2004; Sasa et al., 2009; Nunes et al., 2010; Matias et al., 2011; Henao-Duque and Ceballos, 2013; Leão et al., 2014). Because allometric ontogeny is consistent among sexes, and because size-free shape differences are rather small, Sexual Shape Dimorphism (SShD) in the head is largely generated by differential growth of the head between sexes.

In some snakes, the larger size in adult females has been associated with fecundity selection, with a positive correlation between female size and larger offspring and/or larger numbers of eggs (e.g. Shine, 1989, 1994; Solórzano and Cerdas, 1987, 1989; Janeiro-Cinquini and Leinz, 1990; Janeiro-Cinquini, 2004). It is known that larger offspring have higher survival rates and can store more yolk

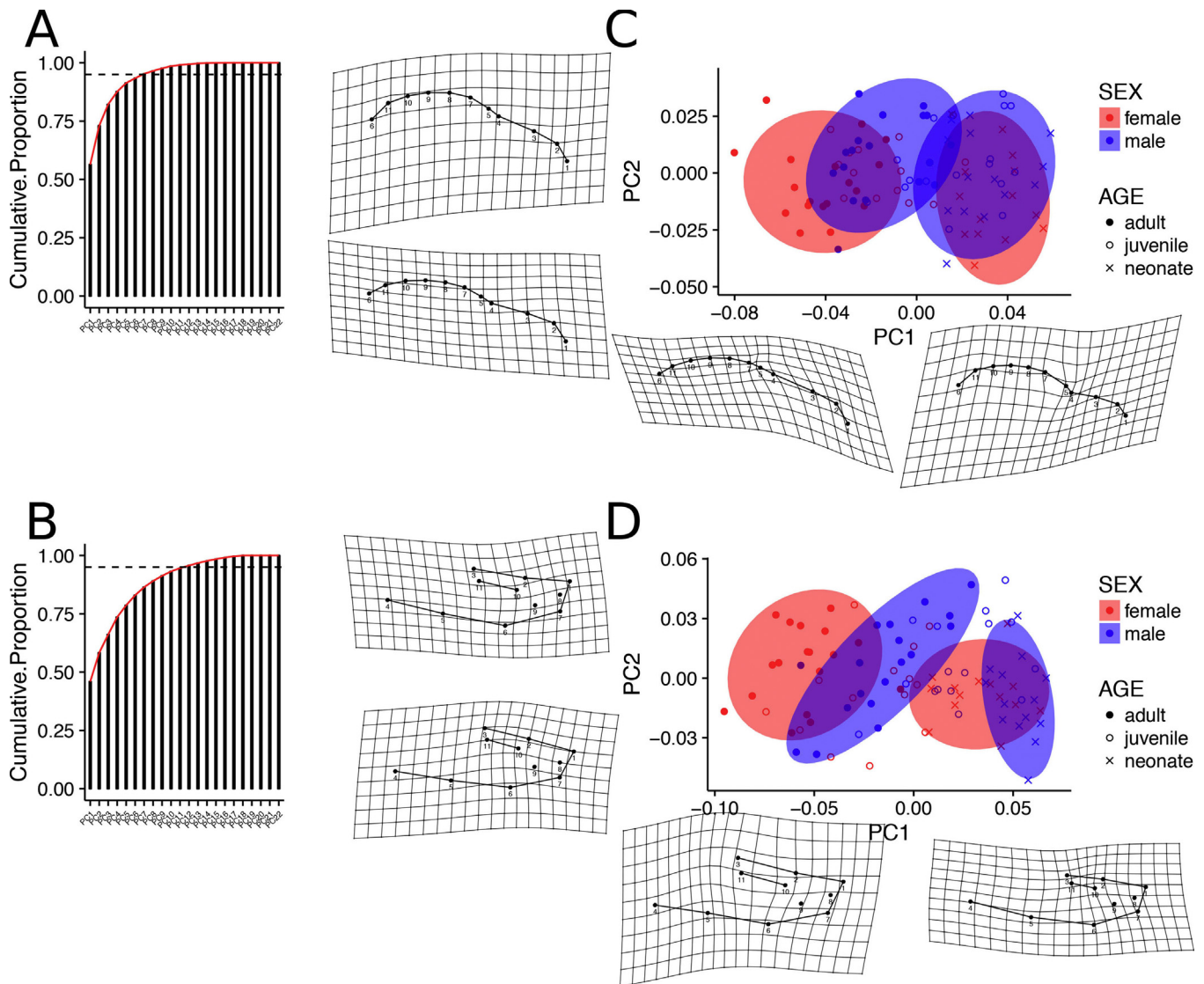


Fig. 4. Principal Component Analysis of Shape Variables (Procrustes residuals) of *Bothrops atrox* head in dorsal and lateral views. A and B- Distribution of Accumulative proportion of variance explained by successive PC axis for dorsal and lateral views, respectively. C and D- Distribution of sexes and age classes on the first two principal components for dorsal and lateral views, respectively. The splines represent positive and negative shape extremes for each axis.

or fat for their development (Ford and Seigel 1989). On the other hand, males generally show relatively longer tails than females to accommodate the hemipenis and retractor muscles related to that organ, as well as to gain advantage during mating courtship (King, 1989; Shine, 1993; Greene, 1997). In some species, males become mature with smaller body size than females and decrease their growth rates after reaching maturity, resulting in sexual dimorphism in advanced stages of life (see Shine, 1990, 1993).

Our geometric morphometrics analyses revealed that SShD was related to changes in head robustness (in dorsal view) and mouth relative size (in lateral view) with females having more robust heads and wider mouths than males. Differences in head and mouth dimensions might have important ecomorphological implications, as many studies have shown that natural selection acting to reduce resource competition between the sexes may also be an evolutionary force driving sexual dimorphism (e.g. Slatkin, 1984; Shine, 1989; Shine et al., 1998). In snakes, head size is important for feeding because they are considered gape-limited predators. The size of the head and consequently the opening of the mouth would limit the potential size of the prey (Shine, 1991). According to Shine (1989, 1991), in species with marked sexual dimorphism in body

size, dietary ecology for males and females are unlikely to be the same. Whereas sexual selection could have produced overall differences in size, intraspecific competition and natural selection can help to maintain sex differences by disruptive selection on allometric shape changes, allowing the sexes to exploit differently shaped prey (Camilleri and Shine, 1990; Shine, 1991; Vincent et al., 2004a, 2004b).

Henao-Duque and Ceballos (2013) observed that females of *Bothrops asper* (Garman, 1883) had larger heads and disproportionately faster growth rates than males. They found evidence of sexual differences in head size and shape even with individuals raised on the same diet, suggesting that this is not due to phenotypic plasticity, being probably genetically determined. Our results show that females are actually born with proportionally larger heads, a fact that is consistent with both head size and shape differences being genetically determined. Because head shape was mostly dependent on head size, then if diet depends on head shape, we would have to conclude that intraspecific competition is present throughout the life history of *B. atrox*, with larger males competing for resources with slightly smaller females.

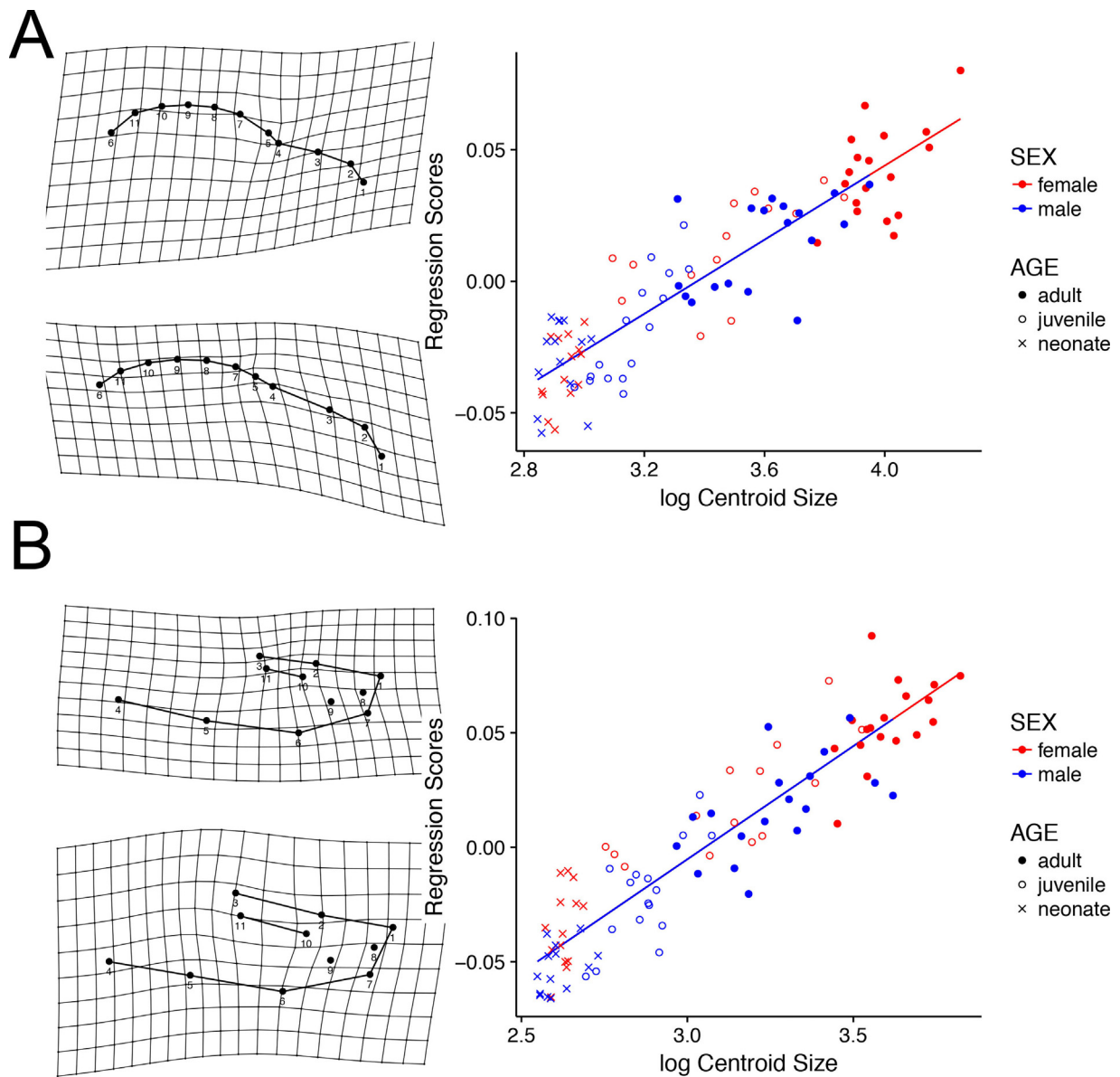


Fig. 5. Relationship between regression scores on logCS of head shape variation in dorsal (A) and lateral (B) view of the head of *Bothrops atrox*.

A similar pattern was found by Meik et al. (2012), who evaluated the relationship between sexual divergence in diet and head morphology in the rattlesnake *Crotalus polystictus* (Cope, 1865), indicating that males have wider heads than females, but both adult males and females feed predominantly on mice and voles. Because of this, the authors suggest that head dimorphism is probably related to different selection pressures on each sex, which in turn were influenced by preexisting body size differences. Even though dietary information of *B. atrox* is scarce, a literature review shows that adult specimens primarily consume the same prey species, mostly mammals (Oliveira, 2003; Bernarde and Abe, 2010; Frota, 2012; Moldowan, 2016. Appendix B, Table S2), similarly to what was observed for *C. polystictus*. Thus, it's probable that both sexes explore similar food items, with females eventually consuming larger mammals (Meik et al., 2012). More studies on the ontogenetic variation in diet and feeding performance are needed to fully understand how allometric differences translate in functional differences, the extend of niche overlap between sexes and their possible consequences.

In regard to ontogenetic changes observed in head shape in neonates and adults of *B. atrox* these may be associated with different types of prey consumed during different stages of growth. The compensation hypothesis, predicted by Carrier (1996), is particularly relevant for the feeding biology of animals that do not mechanically reduce their prey before ingestion, such as snakes, since juveniles have a disadvantage compared to adults because of their small feeding structures (Vincent et al., 2004a). This hypothesis would explain the fact that neonates of *B. atrox* first feed on small and ectothermic prey such as anurans and lizards, whereas adults prey mainly on larger and endothermic prey such as birds and mammals (Martins and Gordo, 1993; Martins and Oliveira, 1999; Macedo-Bernarde and Bernarde, 2005; Frota, 2012. Appendix B, Table S2).

The present study increases our knowledge about the changes in morphology of the head in Neotropical snakes by describing growth patterns and sexual dimorphism in *B. atrox*. Using graphical geometric morphometrics, our results reveal the sexual and ontogenetic changes related to head shape and size. The morphological differences pointed out in this study will be better understood

through future analyses of pre- and postnatal trajectories of skull development.

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Appendix A.

Specimens used in the present study are deposited in the Brazilian scientific collection: Museu Paraense Emílio Goeldi (MPEG), Belém, Pará, Brazil.

BRAZIL: MPEG 20180; Acre: MPEG 20518, Porto Walter: MPEG 19118; Amazonas: Coari: MPEG 23616, Humaitá: MPEG 21255, Itacoatiara: MPEG 23510, MPEG 23512, Manicoré: MPEG 20847, Maraã: MPEG 16779, MPEG 16781, Presidente Figueiredo: MPEG 17464, MPEG 17592, MPEG 17728, MPEG 17732, MPEG 17734, MPEG 17765, MPEG 17766, MPEG 17767, MPEG 17768, MPEG 17769, MPEG 17770, MPEG 17771, MPEG 17772, MPEG 17773, MPEG 17774, MPEG 17775, MPEG 17776, MPEG 17792, São Gabriel da Cachoeira: MPEG 600, MPEG 601; Maranhão: Açailândia: MPEG 25383, Bom Jesus das Selvas: MPEG 25399, MPEG 25400, MPEG 25401, MPEG 25402, MPEG 25403, MPEG 25404, Governador Nunes Freire: MPEG 25906, Nova Vida: MPEG 11067, MPEG 11082, MPEG 14733, MPEG 15728, MPEG 15734, MPEG 15743, MPEG 15748, MPEG 16240, MPEG 16242, MPEG 16244; Pará: Abaetetuba: MPEG 24058, MPEG 25787, Almeirim: MPEG 15168, MPEG 23724, MPEG 23725, MPEG 23727, Altamira: MPEG 23096, MPEG 23098, Ananindeua: MPEG 18765, Anapú: MPEG 22372, Barcarena: MPEG 23403, MPEG 23404, MPEG 23405, MPEG 23409, MPEG 24016, Belém: MPEG 356, MPEG 17623, MPEG 18573, MPEG 18700, MPEG 18749, MPEG 18777, MPEG 18786, MPEG 18787, MPEG 18960, MPEG 18970, MPEG 19024, MPEG 19344, MPEG 19577, MPEG 19579, MPEG 19580, MPEG 19596, MPEG 19654, MPEG 20651, MPEG 19656, MPEG 21041, MPEG 22132, MPEG 22292, MPEG 23116, MPEG 23646, MPEG 23647, MPEG 24273, MPEG 24473, MPEG 24474, MPEG 25009, MPEG 25904, MPEG 26111, Breves: MPEG 17341, MPEG 17342, MPEG 17352, MPEG 17353, MPEG 17354, MPEG 17357, Cachoeira do Piriá: MPEG 26116, Chaves: MPEG 24954, Colônia Nova: MPEG 9506, MPEG 9509, MPEG 11473, MPEG 11972, Conceição do Araguaia: MPEG 19801, Currálinho: MPEG 24408, Dom Eliseu: MPEG 24015, Itaituba: MPEG 21226, MPEG 21227, MPEG 21228, MPEG 21229, MPEG 21258, MPEG 23062, MPEG 24567, MPEG 25161, Juruti: MPEG 20416, MPEG 20426, MPEG 22468, MPEG 22469, MPEG 22470, MPEG 22471, MPEG 22472, MPEG 22473, MPEG 22474, MPEG 22475, MPEG 22476, MPEG 22477, MPEG 22478, MPEG 22479, MPEG 22480, MPEG 22481, MPEG 22482, MPEG 22631, MPEG 22683, MPEG 22695, MPEG 23276, MPEG 23277, MPEG 23278, Marabá: MPEG 19379, MPEG 23806, MPEG 23807, MPEG 24279, MPEG 25382, Melgaço: MPEG 21632, MPEG 21634, MPEG 21635, MPEG 21636, MPEG 21638, Óbidos: MPEG 23648, MPEG 23650, MPEG 23651, MPEG 23652, Oriximiná: MPEG 20178, MPEG 20179, MPEG 20786, MPEG 21558, MPEG 22161, Ourém: MPEG 3523, MPEG 4225, MPEG 4236, MPEG 5530, MPEG 5531, MPEG 7032, MPEG 7041, MPEG 18863, MPEG 21208, MPEG 21209, MPEG 21210, MPEG 21292, Paragomi-

nas: MPEG 21342, Portel: MPEG 23171, MPEG 23173, MPEG 23174, Santa Bárbara: MPEG 19670, MPEG 20263, MPEG 23586, Santarém: MPEG 19057, MPEG 24495, MPEG 24496, MPEG 25388, São Geraldo do Araguaia: MPEG 18967, São Sebastião da Boa Vista: MPEG 18414, Tucuruí: MPEG 18581, Vigia: MPEG 4710, MPEG 8474, MPEG 8532, Viseu: MPEG 9821, Vitória do Xingu: MPEG 19860, MPEG 22375, MPEG 26215; Rondônia: Porto Velho: MPEG 25502, MPEG 25504, MPEG 25505, MPEG 25506, MPEG 25508, MPEG 26044

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.jcz.2017.11.001>.

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