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MORPHOLOGICAL VARIATION IN *BOTHROPS JARARACA AND B. INSULARIS*: SEXUAL DIMORPHISM AND ONTOGENY

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Financiadora: CAPES

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São José do Rio Preto
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Dedico a minha família e meus amigos mais próximos que foram pilares sem os quais este trabalho não estaria de pé

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“[...] Venha, o amor tem sempre a porta aberta

E vem chegando a primavera

Nosso futuro recomeça

Venha, que o que vem é perfeição.”
(Legião Urbana, 1993)

RESUMO

A morfologia é um dos traços mais variáveis nas serpentes. Ela é altamente correlacionada a vários traços biológicos e também a pressões ambientais. Usei duas técnicas complementares, morfometria linear e geométrica, para avaliar a variação morfológica em *Bothrops jararaca* e *B. insularis* dentro, e entre populações e espécies, para testar o efeito do dimorfismo sexual, distribuição geográfica e tendências microevolutivas. Medi entre 11 a 17 variáveis lineares de cada indivíduo. Além disso, 19 landmarks anatômicas foram posicionadas na cabeça, usando uma imagem fotográfica da vista dorsal. Em *B. jararaca*, fêmeas foram geralmente maiores para as medidas do corpo e da cabeça, ao passo que machos foram maiores para as variáveis da cauda. Encontrei efeito significativo da população, sendo que a população do planalto alcançou maiores tamanhos do que no litoral, e fêmeas apresentaram a cabeça com uma região pós-occipital em formato de flecha. Ambas as populações mostraram marcada alometria ontogenética, e a trajetória variou para cada traço medido. Um padrão de dimorfismo sexual similar ocorreu em *B. insularis*, mas não houve diferença no formato da cabeça, porém machos apresentaram olhos maiores. Os sexos tiveram trajetória ontogenética sobreposta para o formato do corpo, mas com inclinação diferente para o formato da cabeça. Comparações interespecíficas indicaram uma cabeça mais comprida e com focinho mais proeminente em *B. insularis*, mais similar à da população do planalto. A trajetória ontogenética também foi paralela com a do planalto e convergente com a população do litoral. A partição de nicho é uma explicação a para algumas das diferenças dos padrões aqui detectados. Da mesma forma, a disponibilidade de presas e ecologia comportamental podem produzir diferentes fenótipos em cada população ou espécie. Atribuo as diferenças na trajetória ontogenética principalmente à eventos de maturação heterocrônica e variação temporal nas mudanças ontogenéticas.

Palavras-chave: Jararaca. Forma. Morfometria geométrica. Alometria. Jararaca-Ilhoa.

ABSTRACT

Morphology is one of the most variable traits in snakes. It is highly related to several biological traits and also environmental pressures. I used two complementary techniques, linear and geometric morphometrics, to evaluate morphological variation in *Bothrops jararaca* and *B. insularis* within and among populations and species, to test the effects of sexual dimorphism, geographic distribution and microevolutionary trends. I measured from 11 to 17 linear variables from each individual. Moreover, 19 anatomical landmarks were placed in the head using a photographed image of the dorsal view. In females were generally larger than males for body and head measures, while males were larger for tail variables. I found a significative effect of population, being that the highland population reached larger sizes than coastal population, and females presented a larger post-ocular region and a more arrow shaped head. Both populations showed a marked ontogenetic allometry and ontogenetic trajectory varied depending on each variable. A similar sexual dimorphism pattern occurred in *B. insularis* body, but with no difference in head shape, however males had larger eyes than females. Sexes had overlapped ontogenetic trajectory in body shape, but with different slopes in head shape. Interspecific comparisons indicated a longer head and prominent snout in *B. insularis*, closer to the highland population. Ontogenetic trajectory also was parallel with highland and convergent with coastal population. Niche partitioning is an explanation for the differences in the observed patterns. Accordingly, prey availability and behavioral ecology may produce different phenotypes on each population or species. I attribute differences in ontogenetic trajectories mainly due heterochronic maturation events and different onset on ontogenetic changes.

Keywords: Pitviper. Shape. Geometrical morphometrics. Allometry. Golden Lancehead.

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LIST OF ABBREVIATIONS AND ACRONYMS

A.S.L. – Above sea level

IBSP – Instituto Butantan São Paulo

SVL – Snout-vent length

VS – Ventral scales

SS – Subcaudal scales

TL – Tail length

TW – Tail width

MW – Middle width

HW – Head width

DBE – Distance between eyes

DBL – Distance between loreals

DBN – Distance between nasals

DEN – Distance eye to nasal

DEL – Distance eye to loreal

DLN – Distance loreal to nasal

HL – Head length

DRL – Distance rostral to labial

HH – Head height

ED – Eye diameter

F – Female

M – Male

SDI – Sexual dimorphism index

LDA – Linear discriminant analysis

ANOVA – Analysis of variance

ANCOVA – Analysis of covariance

PCA – Principal component analysis

CS – Centroid size

MANOVA – Multivariate analysis of variance

SSD – Sexual shape dimorphism

BC – Body circumference

RLD - Rostrum-labial Distance

QGI – Queimada Grande island

Regscore – Regression score

RTL – Relative tail length

MAT – Mean annual temperature

MAP – Mean annual precipitation

SUMMARY

GENERAL INTRODUCTION

Extant snakes are characterized by a unique morphology related to others vertebrates. It has an elongated and cylindrical body associated to a multiplication in body vertebrae and an almost total reduction on limbs and girdle elements, which are most attributed to an evolution to a more terrestrial than aquatic habits (Apesteguías and Zaher 2006; Müller et al. 2010). Thereby, one may mistakenly think that snakes have a simplified morphology with little variation, however several studies have shown otherwise, with a large variation in size and shape mainly attributed to their functional biology, phylogenetic relationships and ecological pressures (Gans 1961; França et al. 2008; Hampton 2011; Esquerré and Keogh 2016).

In reptiles, morphological variation is expected not only on large scale, but occur in closely related species (Zamudio 1998; Wüster et al. 2005), and even intraspecifically, among sexes (Camilleri 1990; Shine and Shetty 2001; Brown et al. 2017) or populations (Hoge et al. 1976; Zamudio 1998; Shine et al. 2012). Body size, the most prominent morphological trait, is often biased toward the sex that receive advantage for being larger (Shine 1994). For example, females are larger due an increase in fecundity, and males are the large sex when male-male combat is present (Shine 1978; Shine 1993; Shine 1994). On the other hand, the ecological hypothesis also provides good explanation for sexual dimorphism. Sexes often diverge due a niche partitioning, such as diet or habitat use, accordingly, the sex that consume larger prey often attain larger sizes (Shine 1986; Shine and Fitzgerald 1991; Shine 1998; Cox 2007). Although body size be the most studied trait, dimorphism also occur in a variety of other traits, such as tail and head size and shape, scalation and coloration (Shine 1993; Shine 1991; Shine and Shetty 2001).

The hypothesis stated above also account for morphological variation between populations of the same sex and also for sexual dimorphism degree. In Australia the python *Morelia spilota* is widespread all over mainland and islands and, unusually among reptiles, populations diverge in mating systems, being that populations of northeast, males present combat and are larger than females, whereas in southeast, no evidence of combat are known and females grew twice than males and reach almost 10 times their mass (Shine and Fitzgerald 1995; Pearson et al. 2002a). Furthermore, comparing populations with a single mating system (no combat), females were always larger than males, however the degree of sexual dimorphism greatly varies, associated mainly with prey resources in each population (Pearson et al. 2002b).

Sexual dimorphism is rather studied in samples composed only by adult specimens, however a comprehensive analysis on postnatal ontogenetic growth is important to understand the onset of diversification as sexes may have different growth rates and size/age at maturation (Beaupre et al. 1998; Taylor and Denardo 2005; Pearson et al. 2002a). Additionally, several traits exhibit a significative allometric association with size, and differences in sex, population or species may rise as differences in ontogenetic trajectories (Scanferla 2016; Strong et al. 2019). Accordingly, patterns of allometry are strongly related to species phylogeny and ecology, such as diet, foraging behavior and habitat use (Taylor and Denardo 2005; Urosevic et al. 2013; Sherrat et al. 2019).

Notwithstanding, phenotypes may diverge even in overlapped allometric trajectory, through heterochronic events. In its seminal review, Klingenberg (1998) argued about the concept of heterochrony, and although it is still under discussion, from a developmental point of view, heterochrony may be summarized as changes in rate and/or timing of ontogenetic allometries between groups. Heterochrony is the proximate cause responsible for several cases of morphological variation, being that groups may be paedomorphic or peramorphic in relation to each other (Klingenberg 1998; Piras et al. 2011). In snakes, heterochronic processes are known to drive phenotypical convergence or divergence even in megadiverse clades, as the skull shape of microcephalic sea snakes (Sherrat et al. 2019) and the body and head shape of pythons (Esquerré et al. 2017).

In Brazil, the pit vipers of the genus *Bothrops* are one of the most diverse. About 30 species are recognized and are widespread in all country (Costa and Bérnils 2018; Nogueira et al. 2019). The rapid diversification rates and radiation of the pit vipers to the New Word in late Oligocene and early Miocene (Alencar et al. 2016), enabled the occupation of several niches, and consequently, morphological adaptations (Alencar et al. 2016; Alencar et al. 2017). Species with enhanced arboreal habits are generally in intermediate sizes, are slander bodied and present larger tails than terrestrial species (Martins et al. 2001; Alencar et al. 2017). Also, there is a broader variation in diet of pit vipers, with a wider range of prey types, generalist or specialist species, and presence or absence of a conspicuous ontogenetic change (Martins et al. 2002). Females are usually larger, and no male-male combat are rare (Barros et al. 2020). In this group, two species have been the subject of several researches, the common lancehead *B. jararaca* and its sister clade *B. insularis*, yet, little is known about morphological variation and developmental processes in these two species.

BOTHROPS JARARACA

The common jararaca *Bothrops jararaca* is a medium sized pit viper that reaches until 1,600 mm in total size (Campbell and Lamar 2004). It is widely distributed in South America, occurring in Paraguay, Argentina, and in Brazil, from Rio Grande do Sul to southern Bahia (Campbell and Lamar 2004; Nogueira et al. 2019). This species horizontally, inhabits mainly the Atlantic Forest, however may occur in open areas and even in modified and highly urbanized regions, and vertically from sea level up to 1,200m A.S.L. (Puorto et al. 1991; Marques et al. 2019; Nogueira et al. 2019). B. jararaca is largely a nocturnal species and may be found almost the entire year, although show a seasonal peak of activity during the rainy season (Sazima 1992; Campebell and Lamar 2004; Siqueira et al. 2021).

The species pass through a marked ontogenetic change in diet, with juveniles feeding mostly on frogs such as *Hylids* and Leptodactylids, however small rodents, lizards and centipedes are also eaten less frequently, and as adults rely mainly on small rodents (Sazima 1992; Marques et al. 2019). Ontogenetic changes are also evident in some morphological traits, such as tail tip color, that are often white or yellowish contrasting with the body color in juveniles and are used as a bait to attract ectothermic prey such as frogs and lizards, and the tail become suffused as snake grows (Sazima 1991; Sazima 1992; Martins et al. 2002). B. jararaca is an ambush predator that probably actively forage occasionally (Sazima 1992). Juveniles usually bite to envenom and hold their harmless prey to avoid them to scape (frogs jumps and chemical clues became difficult to follow), however, adults face usually more dangerous species, therefore release the prey after the bite, and follow chemical clues to find them after subjugation (Sazima 1989; Sazima 1991; Hartman et al. 2003).

Females are larger and heavier than males (Sazima 1992; Matias et al. 2011), have a larger head and smaller tail (Wüster et al. 2005). A previous study also indicates that morphology may vary between population, with a trend of larger females in a small and urbanized fragment than in larger and connected one (Siqueira et al. 2018). Females usually mature at larger sizes than males (750 mm for females and 650 mm for males), and growth rates vary from 5 to 18 mm monthly, but no sex differences are known, and life span are estimated from 10 to 12 years (Sazima 1992).

BOTHROPS INSULARIS

The golden lancehead *Bothrops insularis* is an insular species endemic on Queimada Grande island, located about 33 kilometers far from the Southwestern Brazilian coast (24° 30' S, 43° 42' W; Duarte et al. 1995). The island is considered an inhospitable place due its inaccessibility and hostile environment with no fresh water spring and the presence of the venomous and snake (Amaral 1921b; Duarte et al. 1995). Although *B. insularis* appears to be abundant relatively with any other continental snake, the first populational estimative was below those once speculate in literature (less than 2500 individuals in the island; Martins et al 2008). Unfortunately, few years later a detailed demographic survey found evidence for a populational decline trend (Guimarães et al. 2014), which brought new concerns about the species knowledge and conservation. The endemism, small island area (430,000 m²) with suitable habitat, populational decline, and biopiracy make this snake one of the most threatened species in the entire word (Marques et al. 2004).

The most accepted hypothesis for the origin of the species is that *B. insularis* share a common ancestor with its sister clade B. jararaca. About 11,000 years ago, in the quaternary period, a glaciation has enhanced the sea level, isolating one population of the ancestor on what would be today, the Queimada Grande island, and due different selective pressures of the mainland, the island population suffered an allopatric speciation (Marques et al. 2002; Wüster et al. 2005). The golden lancehead has a more diurnal and arboreal habits than the general in the genus *Bothrops* (Amaral 1921; Amaral 1921b; Marques et al. 2019). It feeds on small ectotherms as juvenile, such as centipedes and small frogs, and whereas adults, rely most on migratory passerine birds that visit the island twice a year, moreover, its ontogenetic shift in diet is less conspicuous than B. jararaca (Martins et al. 2002; Marques et al. 2012).

Several morphological adaptations have accompanied the increased arboreal habits, such as smaller size, larger tail and slender body than the mainland sister species (Martins et al. 2001; Alencar et al. 2017). Due to morphological constraint, this species matures at small sizes and produces small clutches (Marques et al. 2013). Also, the feeding apparatus is adapted to its feeding habits, such as the larger head and smaller fangs than B. jararaca (Wüster et a. 2005). Sexual dimorphism includes a female biased body, head and fang length, and also an anteriorly positioned hearts, and males had a larger tail (Wüster et a. 2005; Marques et al. 2013).

In this work we use linear and geometric morphometric techniques to analyze morphological variation in *B. jararaca* and *B. insularis*. Specifically, we test hypothesis that there are morphological disparities in adult body and head shape between sexes, populations and species. Also, we seek for ontogenetic scaling in several morphological traits and test for differences in allometric trajectories between groups.

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