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Insights on the reproductive biology of *Oxyrhopus petolarius* (Linnaeus, 1758) (Dipsadidae: Pseudoboini) from Southeastern Brazil

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ABSTRACT

Reproductive biology in snakes can exhibit various forms, ranging from highly seasonal to aseasonal patterns, as well as asynchronous or synchronous behaviors between males and females. Understanding these aspects is a crucial step in comprehending an organism's life history and the evolutionary biology of the species, as it is vital for species conservation. In this study, we examined the reproductive aspects of *Oxyrhopus petolarius* (Linnaeus, 1758) using morphometric and histological data. We observed that females exhibit larger body sizes than males, resulting in Sexual Size Dimorphism (SSD) of 0.41. Females seem to follow a discontinuous reproductive cycle, exhibiting a reproductive period during the rainy season. On the other hand, males exhibit a continuous cycle, with heightened testicular development during the dry season.

Key Words: Continuous cycle; Histomorphology; Tropical snakes; Reproductive patterns; Sexual dimorphism.

The understanding of the reproductive biology of snakes has significantly advanced in the last two decades, with a substantial increase in studies focusing on neotropical snakes, not limited to North American snakes (Shine, 2003; Almeida-Santos *et al.*, 2014). However, much remains to be elucidated, particularly concerning the integration of male and female reproduction (Almeida-Santos *et al.*, 2014). Snakes inhabiting temperate zones typically follow a seasonal reproductive cycle, while those in tropical zones may employ different strategies due to warmer and more stable climates (Shine, 2003; Mathies, 2011). Despite these known patterns, snake reproductive biology exhibits considerable variation, ranging from seasonal (e.g., Rojas *et al.*, 2013) to aseasonal (e.g., Pizzato and Marques, 2002), with variable degrees of temporal coordination between male and female cycles (Mathies, 2011).

These diversities reflect distinct facets of a species' biology and evolutionary history, shaped by complex ecological interactions and environmental factors influencing them (Shine, 2003; Pizzatto *et al.*, 2008). Furthermore, the term 'reproductive biology' encompasses a spectrum of traits, including reproductive cycle, fecundity, sexual maturity, sexual dimorphism, mating systems, and reproductive behaviors. All of these aspects are essential for a comprehensive understanding in the investigation of snake reproductive biology (Almeida-Santos *et al.*, 2014).

The false coral snake, *Oxyrhopus petolarius* (Linnaeus, 1758), is a medium-sized snake belonging to the Pseudoboini tribe, (MacCulloch *et al.*, 2009; Uetz, 2022). This species ranges from southern Mexico to Argentina's Misiones province (Beconi and Scott, 2014; Nogueira *et al.*, 2019). It primarily feeds on

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lizards, inhabiting open and forested environments while foraging on the ground and in vegetation (MacCulloch *et al.*, 2009). Despite limited knowledge regarding its reproductive biology, anecdotal records exist about mating, sexual dimorphism, clutch size, and maturity (Test, 1966; Lynch, 2009; Zacariotti and Valle, 2010; Eversole *et al.*, 2014). Therefore, due to the lack of data on its reproductive biology, here we provide insights into maturity, sexual size dimorphism, reproductive cycle, fecundity, and seasonal activity.

We examined 37 specimens (11 females, 17 males, and 9 juveniles) of *Oxyrhopus petolarius* deposited in the collection of the Museu de Zoologia João Moojen (MZUFV) at the Universidade Federal de Viçosa, Minas Gerais, Brazil, between 1983 and 2018. They originate from the Zona da Mata region, Minas Gerais, and one record (MZUFV2506) is from Bandeira, Minas Gerais. Both are situated within the Atlantic Forest biome (Fig. 1). The Zona da Mata region is characterized by secondary forests located on hilltops surrounded by pastures or plantations (Ribeiro *et al.*, 2011). The climate in these regions is tropical humid, with a rainy season lasting from October to March and the dry season from April to September (de Sá Júnior *et al.*, 2012; INMET, 2022).

To assess maturity, sexual size dimorphism, and fecundity, we first measured five morphological structures from each individual: snout-vent length (SVL) and tail length (TL) ; distance between the eyes (ED), head width (HW), and head length (HL; from rostral scale to retroarticular process), using a digital caliper (accuracy of 0.01 mm); body mass (BM) using an analytical balance. Following Dowling (1951), we counted ventral scales (VS) and subcaudal scales (SCS). Subsequently, we determined the sex of each individual and removed the gonads (posterior infundibulum, non-glandular uterus, and right testis) through a ventral incision for histological analyses (Fig. 2). We measured the largest follicle's diameter (FL), quantified the follicle number (FN), and assessed the oviduct morphology, specifically examining the presence or absence of "folds" (Almeida-Santos *et al.*, 2014). Additionally, we measured the testis diameter and evaluated the duct and testis morphology, looking for opacity and convolution in the duct and size and turgidity in the testis (Almeida-Santos *et al.*, 2014). Testicular mass (TM) was measured from the right testis using an analytical balance. Length, width, and thickness were measured using a digital caliper (accuracy of 0.01 mm) for the calculation of testicular volume (TV) following the ellipsoid formula equation (Rojas *et al.*, 2013). To determine the cost invested in gonads

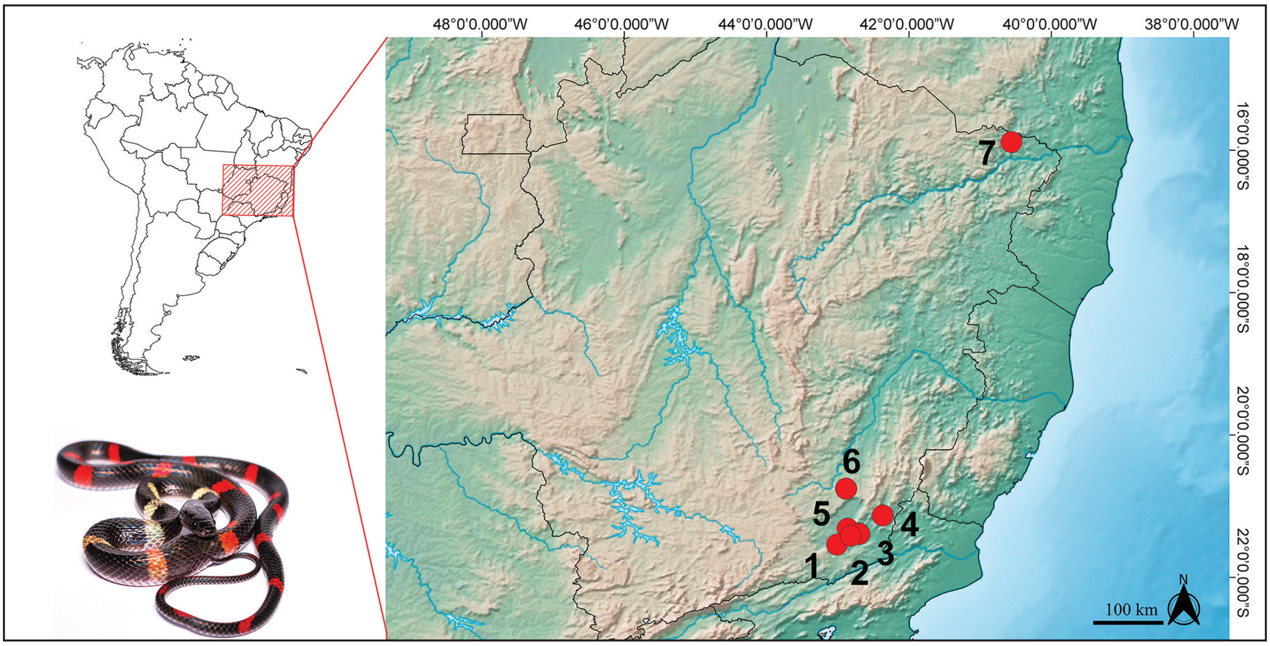

Figure 1. Distribution of the samples of the *Oxyrhopus petolarius* in the municipalities of Zona da Mata, Minas Gerais. 1: São João Nepomuceno – MG; 2: Itamarati de Minas - MG; 3: Cataguases - MG; 4: Muriaé - MG; 5: Astolfo Dutra - MG; 6: Viçosa - MG; 7: Bandeira - MG. Image of a juvenile of *Oxyrhopus petolarius*.

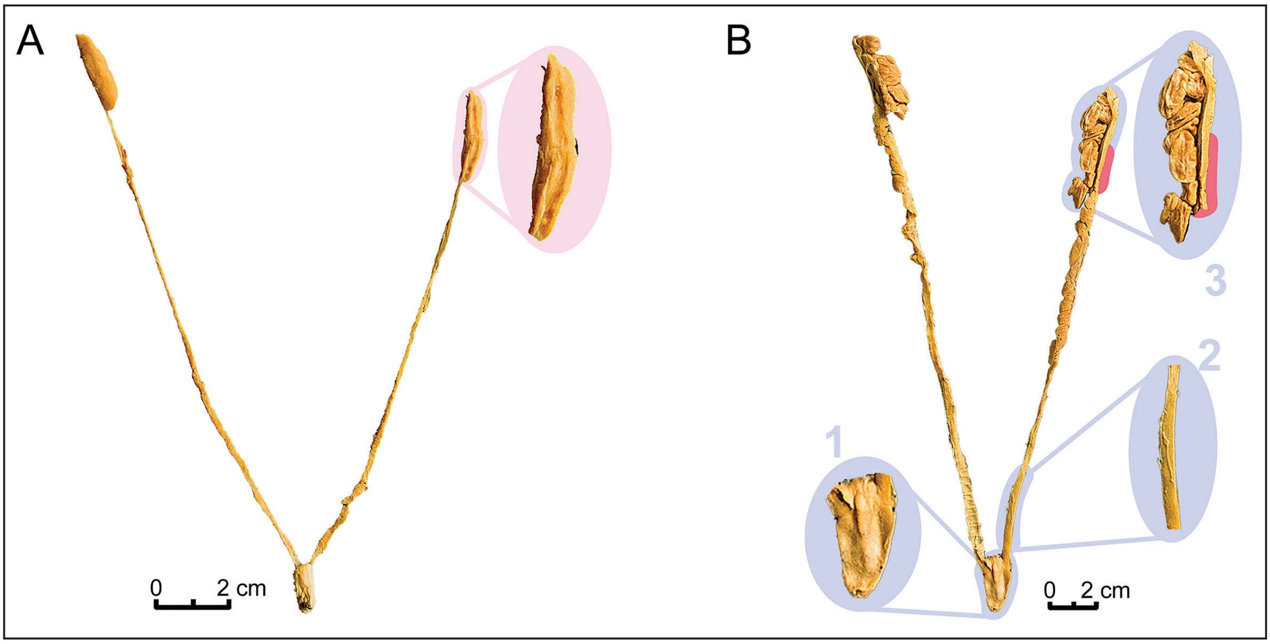

Figure 2. Internal anatomy of the reproductive system of males (A) and females (B) of *Oxyrhopus petolarius*. A: male anatomy with emphasis on testicles; B: female anatomy with emphasis on vagina (1), non-glandular uterus (2), ovary (3), and posterior infundibulum (3 red band).

by males, we determined the gonadosomatic index (GSI) by dividing the mass of the right testis by body mass × 100 (Clesson *et al.*, 2002).

To assess maturity and the reproductive cycle, we used histological analysis. The gonads (posterior infundibulum, non-glandular uterus, and right testis; see Fig. 2A-B), were cut horizontally and dehydrated in an increasing series of ethanol concentrations (70%, 80%, 90%, and 100%). Subsequently, the tissues were embedded in 2-hydroxyethyl methacrylate (Historesin®, Leica) and sectioned at a thickness of 3 μm, maintaining a ten-slice interval between each section. Histological preparations were mounted using Entellan®, and images were obtained under a Leica MC170HD and Olympus Bx53 microscope. We stained the non-glandular uterus and posterior infundibulum with Giemsa to examine the sperm storage. Toluidine Blue staining was used to visualize sperm production in the seminiferous tubules in the testis.

Data analysis was conducted in the R environment, version 4.2.1 (R Core Team, 2022), using exclusively adult specimens. The scripts and data are available on GitHub (https://github.com/rosadolucas/petolarius). Before analysis, we assessed whether the morphological traits are correlated with SVL using a linear regression. We found that all traits are significantly correlated with SVL (available on GitHub). Therefore, to standardize the further analysis, we calculated the ratio between morphological traits and SVL. Principal Components Analysis (PCA) was performed to explore and visualize the morphological spectrum between males and females. To assess the variation in sexual traits, we used ANOVA and T-Student test. For Sexual Size Dimorphism (SSD), we use Gibbons and Lovich's equation, where a positive result indicates females are larger than males, while a negative result indicates the opposite (Gibbons and Lovich, 1990; Shine, 1994).

Sexual maturity in females was determined by the presence of follicles in secondary vitellogenesis or eggs, the presence of sperm in the oviduct, and female size (SVL) (Shine, 1977; Almeida-Santos *et al.*, 2014). We determined the reproductive cycle of females through sperm storage records, the presence of secondary vitellogenesis, copulation records, and oviposition (Shine 1977; Almeida-Santos *et al.*, 2014). Sexual maturity in males was determined by the presence of sperm in the seminiferous tubules, opaque and convoluted deferent duct, and turgid, large testis (Shine, 1977; Almeida-Santos *et al.*, 2014). The male reproductive cycle was determined through sperm production, gonadosomatic index, and copulation records (Shine, 1977; Almeida-Santos *et al.*, 2014).

Juveniles with SVL ≤ 164 mm were classified as neonates. This size was determined based on notes provided by Test (1966), who reported the birth of two *O. petolarius* with 155 and 164 mm in Venezuela. To assess reproductive seasonality, we categorized data into rainy (October – March) and dry (April – September) seasons.

We found six sexually mature females out of 11 examined. The smallest sexually mature female measured SVL = 733 mm (MZUFV2349, collected in August), 65 mm smaller than previously recorded (Eversole *et al.*, 2014), making it the smallest adult female recorded for the species. The largest sexually mature female was collected in October (MZUFV1628) and measured SVL = 970 mm. Out of the 17 males examined, 12 were determined to be sexually mature. The smallest male with sperm production measured SVL = 423 mm (MZUFV1244, see Fig. 3. I). This is the smallest recorded sexually mature male for the species, significantly smaller than the previous record SVL = 610 mm (Eversole *et al.*, 2014). The largest male measured SVL = 703 mm (MZUFV1267). Both specimens were collected in April, the outset of the dry season. The observed difference in size at maturity between males and females suggests that males can achieve reproductive capability at a younger age compared to females (Parker and Plummer, 1987). This distinction is attributed to greater metabolic investment and developmental time required for females before reproduction (Derickson, 1976; Shine, 1994; Bonnet *et al.*, 1998; Shine, 2003). Furthermore, the size of adults at maturity aligns with findings for other species of the genus, such as *Oxyrhopus guibei*, *O. clathratus*, *O. trigeminus*, *O. rhombifer*, and *O. vanidicus* (Pizzatto and Marques, 2002; Gaiarsa *et al.*, 2013; Quintela *et al.*, 2020).

The species exhibit a Sexual Size Dimorphism index of 0.41, notably higher than the 0.18 reported by Shine (1994). These results remain consistent with the broader pattern observed in other snakes from the same tribe and indicate that females are generally larger than males (Pizzatto and Marques, 2002; Pizzatto, 2005; Gaiarsa *et al.*, 2013; Quintela *et al.*, 2020). However, by analyzing the morphology of the traits, it becomes evident that males exhibit larger traits than females (see Table 1). This distinction is further emphasized by the PCA results (Fig. 4) and confirmed by the t-test, which shows a clear separation between males and females.

Follicles in adult females (N = 6) appear to initiate secondary vitellogenesis when reaching a size of ≥ 6 mm, as indicated by the scatterplot (Fig. 5.A). There is a significant difference in follicle size between seasons ($t_{(3.8061)} = -5.4044$, $p = 0.006535$), and body mass ($t_{(3.1921)} = -3.9168$, $p = 0.02642$), with follicles being larger in the rainy season (see Table 1). However, no statistically significant relationship was found between follicle number and SVL ($R^2 = 0.03439$, $F_{(1,4)} = 0.1424$, $p = 0.725$), suggesting that the follicle number does not increase with SVL. The largest follicle measured 13.34 mm (MZUFV1224) and was found in March, at the end of the rainy season, whereas individuals with secondary follicles were collected in March (N= 1), August (N= 1), October (N= 1), and November (N= 1), from the end of the dry season, the outset, and end of the rainy season. The observed correlation with the rainy season is supported by Zacariotti and Valle's (2010) mating observation in October, the outset of the rainy season. Additionally, reports of oviposition by Lynch (2009) at the outset of the rainy season in Colombia and by Test (1966) at the end of the rainy season in Venezuela could imply a pattern of seasonal reproduction for this species. The secondary vitellogenesis recorded in August, during the dry season, and mating observed by Eversole *et al.* (2014) in the dry season (June) may indicate asynchronous reproductive activity among individuals. However, Quintela *et al.* (2020) found both eggs and secondary follicles in the same individual of *O. rhombifer*, indicating that two clutches in the same year are possible for the genus. Sperm storage in April (N= 1; MZUFV1389) (Fig. 3.V-VI), at the outset of the dry season, may be associated with the preference of females to lay eggs in warmer months and the asynchronous reproductive activity among individuals (Vinegar, 1974, Gregory, 2009).

No neonates were found. However, we found four juveniles that are within the range of neonates of *Oxyrhopus guibei* (Pizzatto and Marques, 2002). The smallest juvenile (SVL = 197 mm, MZUFV2190) was collected in October (n = 1), followed by records in February (n = 1; SVL = 229 mm), March (n = 1; SVL = 232 mm), and April (n = 1; SVL = 224 mm). The concentration of juveniles (with the possibility of being neonates) in transition over the seasons may be associated with the availability of prey, as proposed for *O. guibei* (Pizzatto and Marques, 2002). Although not assessed, the diet of *O. petolarius* is generalist, primarily consisting of lizards (Alencar *et al.*, 2013), and during these periods, small lizards are more abundant (e.g., Van Sluys, 1993; Guedes *et al.*, 2022). This phenological association enhances the survival

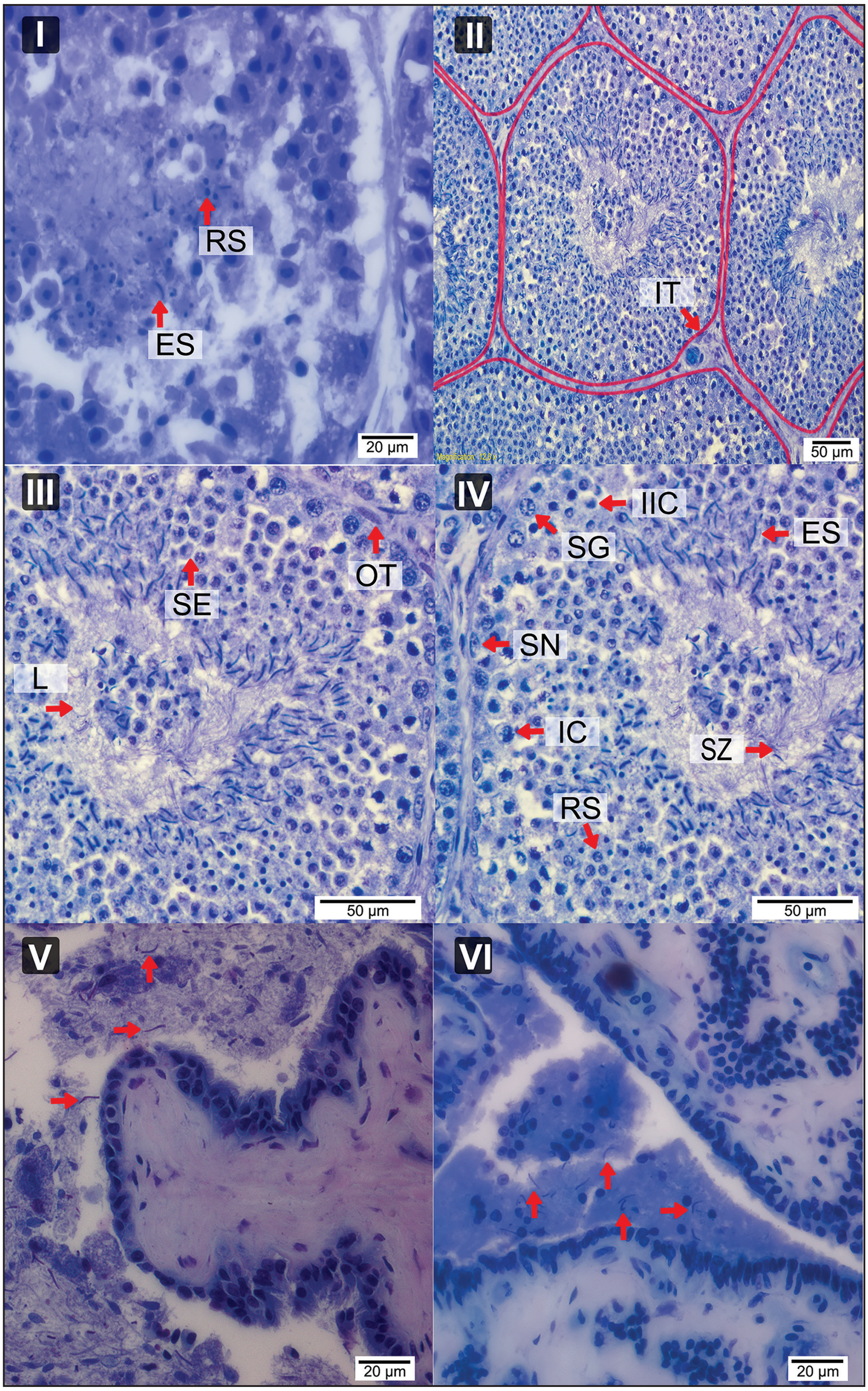

Figure 3. Photomicrograph of the reproductive system of *Oxyrhopus petolarius*. I-IV. Photomicrograph of the testis; I. spermatogenesis inside the testis in the smallest male; II. seminiferous tubule; III and IV. Close-up of the seminiferous tubule; V and VI. Photomicrograph of sperm storage in the non-glandular uterus (V) and posterior infundibulum (VI) of the adult female (MZUFV1389); RS: round spermatid, ES: elongated spermatid. TS: seminiferous tubule; IT: intertubular; OT: own tunic; SE: seminiferous epithelium (germinal); L: lumen; SN: Sertoli cell nucleus; SG: spermatogonia; IC: primary spermatocyte; IIC: secondary spermatocyte; RS: rounded spermatid; ES: elongated spermatid; SZ: spermatozoa; III e IV: zoom of picture II; Red Arrows: indicate sperm in the non-glandular uterus (V) and posterior infundibulum (VI).

Table 1. Mean of relation trait/SVL used in T-test between male and female, and dry and rainy season. F: female; M: male; SVL: snout-vent length; TL: tail length; ED: distance between the eyes; HW: head width; HL: head length; VS: ventral scales; SCS: subcaudal scales; BM: body mass; TV: testis volume; TM: testis mass; GSI: gonadosomatic index; FL: follicles length; FN: follicles number; N: number of individuals; sd: standard deviation; df: degrees of freedom.

Trait	Sex and Season	N	Mean	sd	t	df	p-value
HL	F	6	0.031	0.002	-3.07740	10.9140	0.0106
	M	12	0.348	0.003			
HW	F	6	0.016	0.001	-3.07740	10.9140	0.0106
	M	12	0.019	0.002			
ED	F	6	0.009	0.001	-4.08160	15.9310	0.0009
	M	12	0.011	0.001			
TL	F	6	0.276	0.018	-2.21320	15.2300	0.0057
	M	12	0.327	0.049			
BM	F	6	0.165	0.045	2.83070	8.0591	0.0220
	M	12	0.106	0.245			
VS	F	6	200.660	12.027	2.53860	7.4033	0.0370
	M	12	197.250	4.092			
SCS	F	6	86.500	11.058	-2.00114	10.5620	0.0717
	M	12	97.750	11.600			
TV	dry	8	0.434	0.197	1.7389	7.5119	0.1227
	rainy	4	0.250	0.158			
TM	dry	8	0.000	2.08E-04	2.5963	10	0.0266
	rainy	4	0.000	9.63E-05			
GSI	dry	8	0.361	0.103	0.77255	4.6456	0.4772
	rainy	4	0.299	0.142			
FL	dry	3	5.600	1.263	-5.4044	3.8061	0.0065
	rainy	3	11.937	1.589			
FN	dry	3	19.333	16.165	-0.28029	3.1464	0.7967
	rainy	3	22.333	9.074			
BM*	dry	3	100.667	15.503	-3.9168	3.1921	0.0264
	rainy	3	171.000	26.963			
BM**	dry	8	0.120	0.034	3.3575	8.3578	0.0093
	rainy	4	0.077	0.008			

* female body mass
** BM/SVL of males

of juveniles, as larger lizards may pose risks during consumption attempts (Nogueira *et al.*, 2013; Carilo-Filho *et al.*, 2017).

Adult males with sperm in the lumen were found in the middle of the rainy season (January, N = 1; February, N = 3; see Fig. 5.) and in greater numbers throughout the dry season (April, N = 2; May, N = 2; June, N = 1; August, N = 1; September, N = 1; see Fig. 5). Although the gonadosomatic index (GSI) did not exhibit a statistically significant difference between seasons ($t_{(4.6456)} = 0.77255$, $p = 0.4772$), it was higher in the dry season (0.361 ± 0.103) compared to the rainy season (0.299 ± 0.142). The relationship between testicular volume (TV) and body mass (BM) ($R^2 = 0.7071$, $F_{(1,10)} = 24.14$, $p = 0.0006113$), and testicular mass (TM) and BM ($R^2 = 0.8353$, $F_{(1,10)} = 50.71$, $p = 0.00003$), revealed that larger animals had greater testis volume and mass. Seasonality had a noticeable impact on TM, with greater values in the dry season ($t_{(10)} = 2.5963$, $p = 0.02666$). In contrast, TV did not appear to display strong seasonality ($t_{(7.5119)} = 1.7389$, $p = 0.1227$). It's worth noting that in tropical snakes, rainfall can lead to testicular regression (not assessed in this work),

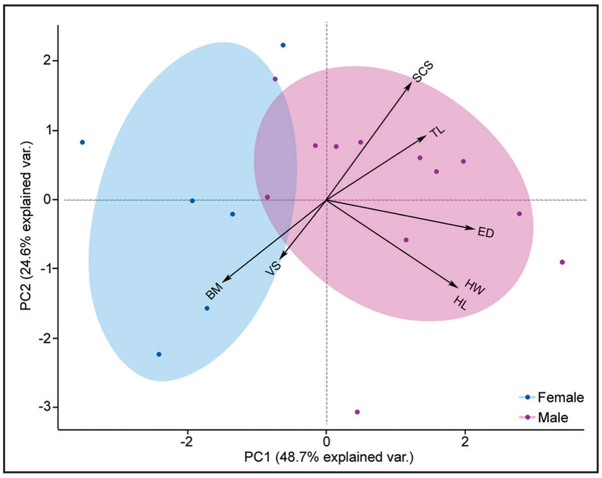

Figure 4. Principal Component Analyses (PCA) show the general pattern of the morphometric variables regarding sex. BM: Body Mass; VS: Ventral Scale; SCS: Subcaudal Scale; TL: Tail Length; ED: Eye Distance; HW: Head Width; HL: Head Length.

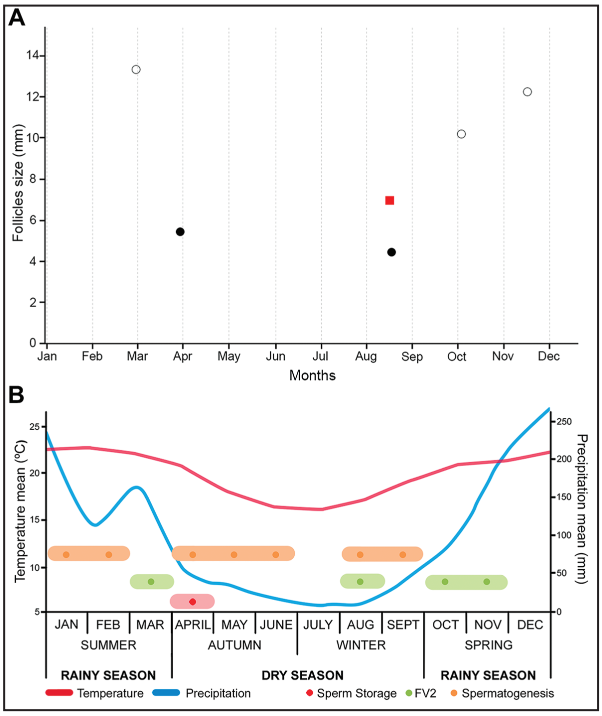

Figure 5. Follicle dispersion of *Oxyrhopus petolarius* (A) and their reproductive cycle summary (B). A: scatter plot of female follicles (n = 9); Red square, the onset of secondary vitellogenesis; Black circle, primary vitellogenesis; White circle, secondary vitellogenesis. B: summary of data obtained regarding the reproductive cycle of females and males; FV2, follicles on secondary vitellogenesis; Precipitation and temperature from 1991 to 2020, from Viçosa-MG

potentially explaining the lower GSI values observed during the rainy season (Krohmer and Lutterschmidt, 2011; Loebens *et al.*, 2017). However, records of sperm production occur throughout the year, suggesting a continuous reproductive cycle (Mathies, 2011).

This study represents the first comprehensive investigation into the reproductive biology of *Oxyrhopus petolarius*, incorporating histomorphometric data to support the predictions. Generally, in species that exhibit sexual dimorphism, females are larger than males. However, in this species males have larger morphological features (Table 1). This could be the result of various forces that we did not assess, such as mate-searching, male-male combat, diet, and niche utilization (Shine, 1986; Bonnet *et al.*, 1998). Females appear to follow a discontinuous reproductive cycle, exhibiting a reproductive period during the rainy season and a peak during the transition from the dry to the rainy season (Fig. 5). This pattern accounts for sperm storage in April, which could be used about four months later. In contrast, males appear to have a continuous reproductive cycle of sexual activity, with enhanced testis development in the dry season, as preparation to mate when females become active. Thus, we propose that the species has a broadly seasonal period of reproduction, as seen in other Xenodontini (Pizzatto *et al.* 2008; Quintela *et al.* 2020). We must emphasize that *O. petolarius* populations may exhibit geographical variations in reproductive traits, since it has a broad distribution, as observed in *Erythrolamprus poecilogyrus* (Pinto and Fernandes, 2004). Thus, a comprehensive and extensive study is essential to fully elucidate the species' reproductive biology.

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