

Natural history of *Xenodon matogrossensis* (Scrocchi and Cruz, 1993) (Serpentes, Dipsadidae) in the Brazilian Pantanal

Hugo Cabral^{1,2,3}, Liliana Piatti⁴, Marcio Martins⁵, Vanda L. Ferreira⁴

¹ Programa de Pós-Graduação em Biologia Animal, Universidade Estadual Paulista, 15054-000, São José do Rio Preto, SP, Brazil.

² Instituto de Investigación Biológica del Paraguay. Del Escudo 1607, Asunción, Paraguay.

³ Mappinguari – Laboratório de Biogeografia e Sistemática de Anfíbios e Répteis, Universidade Federal de Mato Grosso do Sul, 79070-900, Campo Grande, MS, Brazil.

⁴ Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, 79070-900, Campo Grande, MS, Brazil.

⁵ Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, 05508-090 São Paulo, SP, Brazil.

Recibido: 30 Abril 2020
 Revisado: 08 Junio 2020
 Aceptado: 28 Julio 2020
 Editor Asociado: V. Arzamendia

doi: 10.31017/CdH.2020.(2020-026)

ABSTRACT

Xenodon matogrossensis is a neotropical snake restricted to the central part of South America, in the Pantanal wetlands and a few neighbouring areas. The available information about this species in the literature is restricted to geographical distribution, morphological variation and anecdotal information on habitat use. Here we present data on diet, sexual dimorphism and reproduction of *X. matogrossensis*. We gathered information on diet and reproduction from 72 specimens of *X. matogrossensis* deposited in scientific collections. This species feeds mainly on amphibians, but also consumes squamate eggs and other small vertebrates. Mature females are generally bigger than mature males considering body size and head width, but males have longer tail than females. The number of follicles and eggs is not related with body size in females of *X. matogrossensis*. Females showed larger follicle sizes from October to April, however females carrying eggs are found in all stations of the year. The information provided here, associated with others available in the literature can contribute to the assessment of the conservation status of this species and even to design conservation actions in case they are needed in the future.

Key words: Diet; Reproductive Biology; Reptiles; Xenodontinae.

Introduction

Xenodon matogrossensis (Scrocchi and Cruz, 1993) (Fig. 1) is a Neotropical snake distributed in the central part of South America, in the Pantanal wetlands and neighbouring ecoregions (Beni, Cerrado and Chaco Savannas; Scrocchi and Cruz, 1993; Giraudo, 1997; Strüssmann *et al.*, 2011; Cabral *et al.*, 2015). It is a member of a species group within *Xenodon* comprising six species that were previously allocated in the genus *Lystrophis* Cope, 1885 until Zaher *et al.* (2009) synonymized these genera based on molecular evidences. This species group contains *X. dorbignyi* (Bibron, 1854), *X. histricus* (Jan, 1863), *X. nattereri* (Steindachner, 1867), *X. matogrossensis*, *X. pulcher* (Jan, 1863), and *X. semicinctus* (Duméril, Bibron and Duméril, 1854). These species are distributed mainly in open areas of South America and are characterized by having the rostral scale conspicuously keeled (Scrocchi and Cruz, 1993;

Cabral *et al.*, 2015). *Xenodon pulcher*, *X. semicinctus*, and *X. matogrossensis* show mimetic colour patterns with coral snakes of the genus *Micrurus*, while the other species of the group show a predominantly pale ground colour with simple bands or ocelli (Cei, 1993; Giraudo, 2002).

Members of this species group are considered psamphilic, inhabiting open areas with sandy soil, and feed mainly on anurans, lizards, and squamate eggs (Orejas-Miranda, 1966; Gudynas, 1979; Williams and Scrocchi, 1994; Oliveira *et al.*, 2001; Carreira and Lombardo, 2007; Nenda and Cacivio, 2007; Sawaya *et al.*, 2008). Concerning reproduction, there is information only for *X. nattereri*, that probably show seasonal reproduction during the hottest months of the year (Sawaya *et al.*, 2008). However, there is only scarce information about the natural history of *X. matogrossensis* in the literature, being

limited to notes about geographical distribution and scattered information on morphological variation and habitat use (Cabral *et al.*, 2015; Nogueira *et al.*, 2019). Here we present data on diet, sexual dimorphism and reproduction of *X. matogrossensis*.

Material and methods

We examined 72 specimens of *X. matogrossensis* deposited in the Coleção Zoológica de Referência da Universidade Federal de Mato Grosso do Sul (ZUFMSREP). All records are from Mato Grosso do Sul state (See Appendix I, for specimens examined). For each specimen we recorded the sex and the following morphological variables: (1) snout-vent length (SVL), (2) tail length (TL), (3) head length (HL), (4) head width (HW), (5) number of ventral scales (VS), and (6) number of subcaudal scales (SS). Measurements were made with a measuring tape to the nearest millimeter (SVL and TL), and the remaining variables with a dial calliper to the nearest 0,01 mm.

We made a mid-ventral incision to check gut

contents and reproductive characters of the specimens. To describe the diet of *X. matogrossensis* we identified prey remains to the lowest possible taxonomic level, under a stereoscopic microscope. To describe aspects of reproductive biology, we counted and took measures of all follicles or oviductal eggs in females and recorded the length of the largest testis (mm) in males. Sexual maturity in males was determined by the presence of convoluted ductus deferens (Shine, 1982; Almeida-Santos and Salomão, 2002, Pizzatto and Marques, 2002, 2006). Females were considered mature if they had secondary vitellogenic follicles (enlarged and yellowish ovarian follicles), oviductal eggs or folded oviducts (Blackburn, 1998; Mesquita *et al.*, 2013). Minimum size at maturity was estimated as the smallest reproductive individual of each sex. We estimated the maximum potential clutch size by counting the number of secondary vitellogenic follicles, oviductal eggs (counting only eggs, or follicles when eggs were absent), and tested if clutch size is affected by female size. We also recorded if females showed distended or folded middle oviduct macroscopically (Blackburn, 1998; Almeida-Santos *et al.*, 2014), and if males presented turgid testes macroscopically when freshly killed (Pleguezuelos and Fahd, 2004). This data was used to infer the period of reproductive activity (Almeida-Santos *et al.*, 2014).

The degree of sexual dimorphism (SSD index) was calculated as $1 - (\text{mean adult SVL of the larger sex} / \text{mean adult SVL of the smaller sex})$ (Gibbons and Lovich, 1990; Shine, 1994). Positive and negative values of SSD correspond to females larger than males and vice versa, respectively. We used an analysis of variance (ANOVA) to test for sexual dimorphism in SVL and scale counts. The other morphological variables (TL, HL and HW) often vary with body length, so we used SVL as a covariate in an analysis of covariance (ANCOVA) to compare these variables between sexes. We tested for effects of body size (SVL) of females on follicles and number of eggs using regression analyses. Statistical analyses were performed with package *vegan* (Oksanen *et al.*, 2013) in R software (R Core Team, 2019).

Results

Females of *X. matogrossensis* are significantly larger than males (ANOVA $F = 4.16$, $p = 0.049$; Table 1), with an SSD index of 0.15. Additional significant differences between mature males and females were



Figure 1. Individual of *Xenodon matogrossensis* (A) and general view of its habitat at Fazenda Nhumirim, Corumbá, Mato Grosso do Sul state, Brazil (B).

Table 1. Summary of morphological variables of *X. matogrossensis* from Mato Grosso do Sul state, Brazil. Numbers in bold indicate significant differences ($p < 0.05$) between sexes (considering mature individuals).

Morphological Variable	Females N= 33 Mean (Range)	Males N= 39 Mean (Range)
snout-vent length (mm)	294.3 (118-487)	246.2 (115-395)
tail length (mm)	38.21 (15-61)	40.26 (16-67)
head length (mm)	17.26 (9.12-26.30)	14.6 (9.80-23.48)
head width (mm)	11.47 (5.94-18.24)	9.32 (5.78-17.42)
ventral scale	135.5 (132-147)	136 (129-145)
sub-caudal scale	26.82 (23-32)	31.08 (25-42)

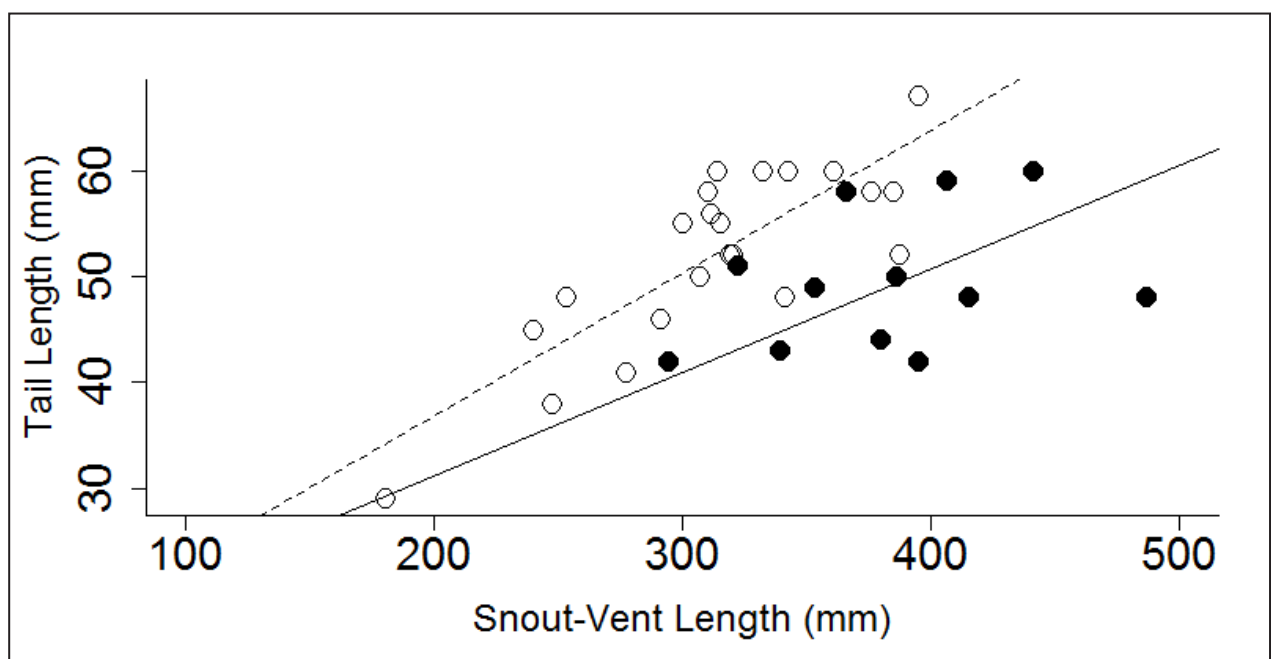
found for tail length (Fig. 2), head width and number of subcaudal scales (ANCOVA $F = 23.49$, $p < 0.001$; ANCOVA $F = 5.06$, $p = 0.031$; ANOVA $F = 24.8$, $p < 0.001$; respectively).

We found 13 females and 22 males with evidence of sexual maturity through the macroscopic analysis of the gonads. Among them, the smallest mature female and male measured 123 mm and 180 mm SVL, respectively. We failed to find a significant effect of female body size on the number of follicles ($r^2 = 0.095$, $F = 3.023$, $p = 0.0983$) or eggs ($r^2 = 0.291$, $F = 1.884$, $p = 0.186$), which varied between 1 and 9 (Fig. 3). As is possible to observe at Figure 3, one of the females was found with 9 eggs, even being much smaller (123 mm SVL) than the other mature females (between 294 and 497 mm, Table 2). Five females presented distended oviduct and

secondary follicles or eggs at the same time (Table 2), what could suggest the occurrence of multiple reproductive events in short periods of time.

The seasonal size variation of follicles and testes of the mature specimens analysed showed that females have secondary vitellogenic follicles from October to April and males have large testes (> 20 mm) from July to December (Fig. 4).

The number of sexually active specimens (if females showing distended or folded middle oviduct macroscopically, and if males presenting turgid testes) was larger than that of sexually inactive specimens between September to February (Fig. 5). Nevertheless, the distribution of body sizes throughout the year suggests that juvenile recruitment occurs from the end of the wet season (March) to the middle of the dry season (July) and in November/

**Figure 2.** Variation in tail length in relation to snout-vent length in males (white dots) and females (black dots) of *Xenodon matogrossensis*.

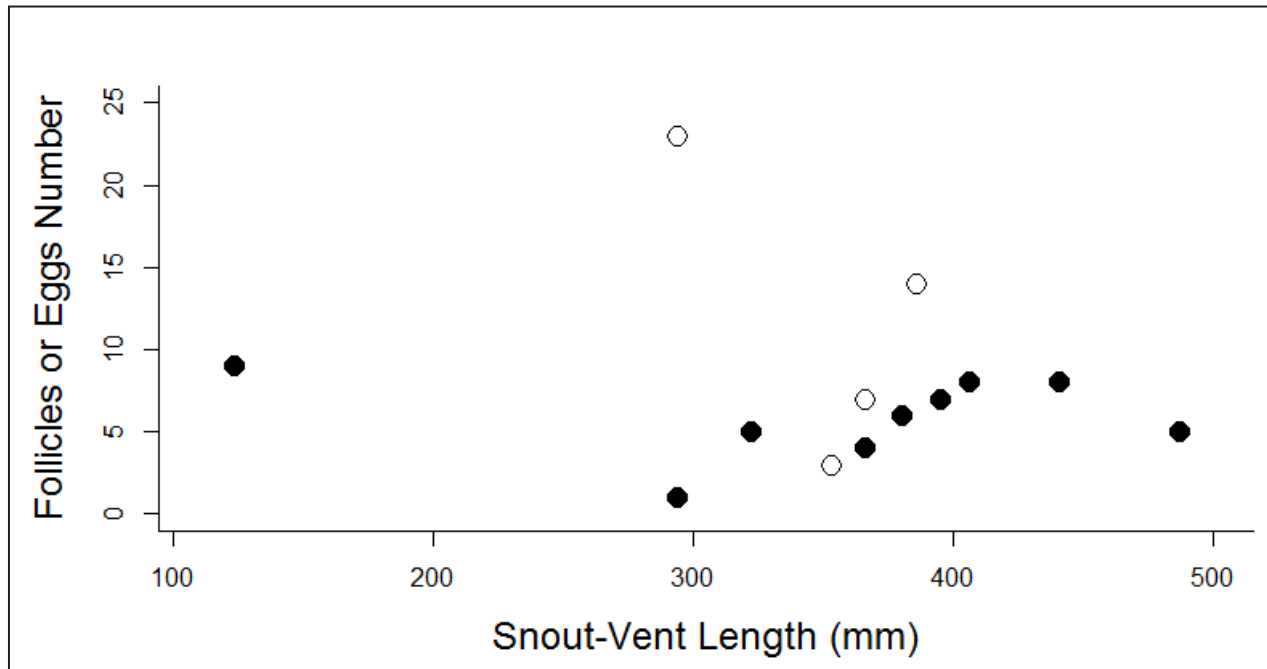


Figure 3. Variation in number of secondary follicles (white dots) or eggs (black dots) in relation to snout-vent length in mature females of *Xenodon matogrossensis*.

December (Fig. 6).

Of the 72 specimens analysed, only eight had prey remains in the gut: five had frog remains, two had elongate squamate eggs and one had bones of an unidentified vertebrate. Among amphibian prey, we were able to identify *Physalaemus nattereri* (Steindachner, 1863) and *Rhinella major* (Müller and Hellmich, 1936) (one record each). We also found

portions of leptodactylid prey in two individuals, as well as digits of an unidentified anuran in one specimen.

Discussion

Our results indicate that *X. matogrossensis* shows the typical natural history features of its species group,

Table 2. Summary of reproductive characteristic of mature females of *X. matogrossensis* from Mato Grosso do Sul state, Brazil. SVL: snout-vent length; FnV: non vitellogenic follicles; Sec. Fol: secondary follicles.

SVL (mm)	Month	FnV	Sec.Fol	Egg	Follicle Size (mm)	Egg Size (mm)	Folded Oviduct
322	Jan	19	0	5	-	17.2	FALSE
353	Jan	0	3	0	8.55	-	TRUE
366	Jan	0	7	4	-	9.55	TRUE
415	Feb	0	0	0	-	-	TRUE
441	Apr	9	0	8	-	16.53	FALSE
123	Sep	0	0	9	-	36.15	FALSE
386	Sep	34	14	0	5.43	-	FALSE
487	Jul	0	0	5	-	31.55	TRUE
294	Dec	24	23	1	-	9.38	TRUE
395	Dec	0	0	7	-	32.67	TRUE
406	Dec	0	0	8	-	23.94	FALSE
339	Nov	0	0	0	-	-	TRUE
380	Nov	0	0	6	-	22.36	FALSE

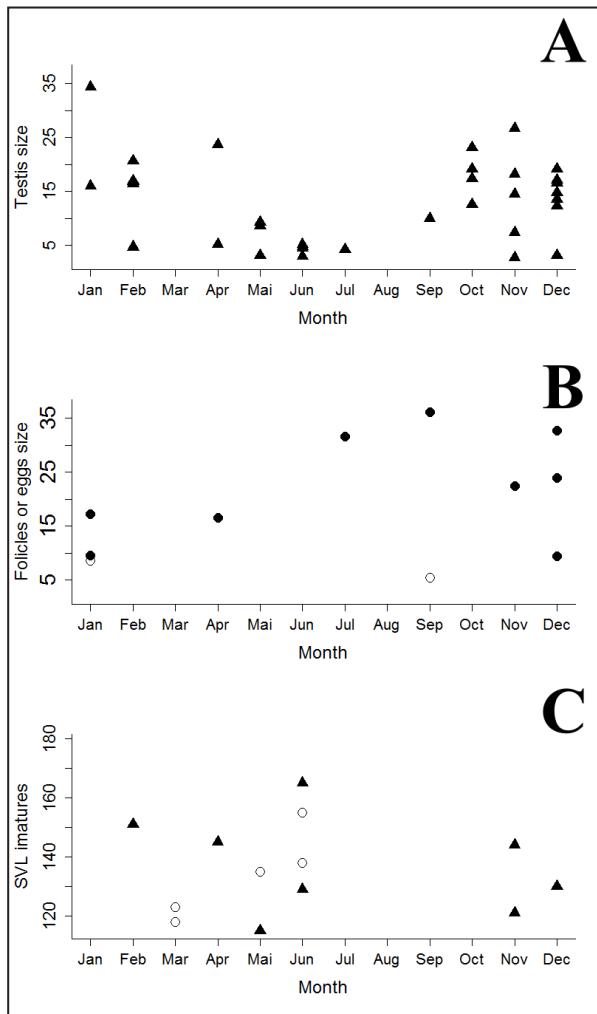


Figure 4. Temporal variation of testis size of mature males (A), secondary follicles (open circles) or eggs (black circles) in females (B) and snout-vent length of immature (C) (triangles: males; circles: females) of *Xenodon matogrossensis*.

formerly assigned to *Lystrophis*: (1) they feed mainly on amphibians, although it also consumes squamate eggs and other small vertebrates; (2) occur in open areas with sandy soils; and (3) they have a seasonal reproduction (Lema *et al.*, 1983; Oliveira *et al.*, 2001; Carreira, 2002).

Females showed large follicle sizes from October to April, suggesting that reproduction may be more frequent during this period, even though individuals may be reproductively active throughout the year. Testes are larger in the first half of the rainy season (October to December), what could be an indicative of higher spermatogenesis activity during this period and another indicative of more reproduction events in this period. However, the lack of histological analyses of testes and a higher number of females collected along the years does not allow us to make strong conclusion about the

reproductive cycle of *X. matogrossensis* here analysed (Almeida-Santos *et al.*, 2014). At the Pantanal region, the period of October to April comprises the hottest and wettest months of the year when several frog species are more active and breed (Prado *et al.*, 2005). This greater availability of prey in conjunction to suitable conditions for high activities of reptiles could favour seasonal reproduction. Oliveira and Martins (2002) suggested that both the snakes and their prey may be responding to the same climatic conditions to breed and seasonal reproduction was reported for snakes from the wetland and dry plain of Pantanal, such as *Micrurus pyrrhocryptus* Cope, 1862 (Ávila *et al.*, 2010), and the viviparous *Helicops leopardinus* (Schlegel, 1837) (Ávila *et al.*, 2006), and *Bothrops matogrossensis* Amaral, 1925 (Monteiro *et al.*, 2006).

The energetic cost of oviparity is lower when compared to viviparity (Gregory *et al.*, 1999; Andrews and Mathies, 2000; Shine, 1980, 1985, 2003), and this lower energy waste might make possible multiple reproduction in the same reproductive season (Almeida-Santos *et al.*, 2014). In this work five females presented distended oviduct and secondary follicles or eggs at the same time, what could suggest the occurrence of multiple reproductive events in short periods of time. Multiple reproductive events were already reported for oviparous populations of Neotropical xenodontines like *Xenodon dorbignyi* (specie closely related to *X. matogrossensis*, Oliveira *et al.*, 2011), *Erythrolamprus poecilogyrus poecilogyrus* (Wied-Neuwied, 1825) (Pinto and Fernandes, 2004), *E. miliaris* (Linnaeus, 1758) (Eisfeld and Vrcibradic, 2019), and other Xenodontini species (Pizzatto *et al.*, 2008). Nevertheless, the condition of show distended oviduct and secondary follicles

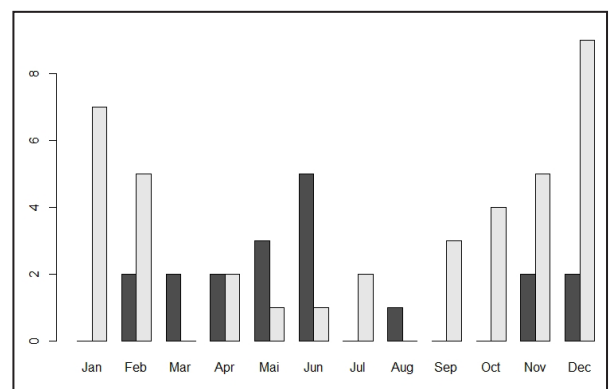


Figure 5. Temporal variation of the occurrence of mature (lighter bars) and immature (darker bars) individuals of *Xenodon matogrossensis*.

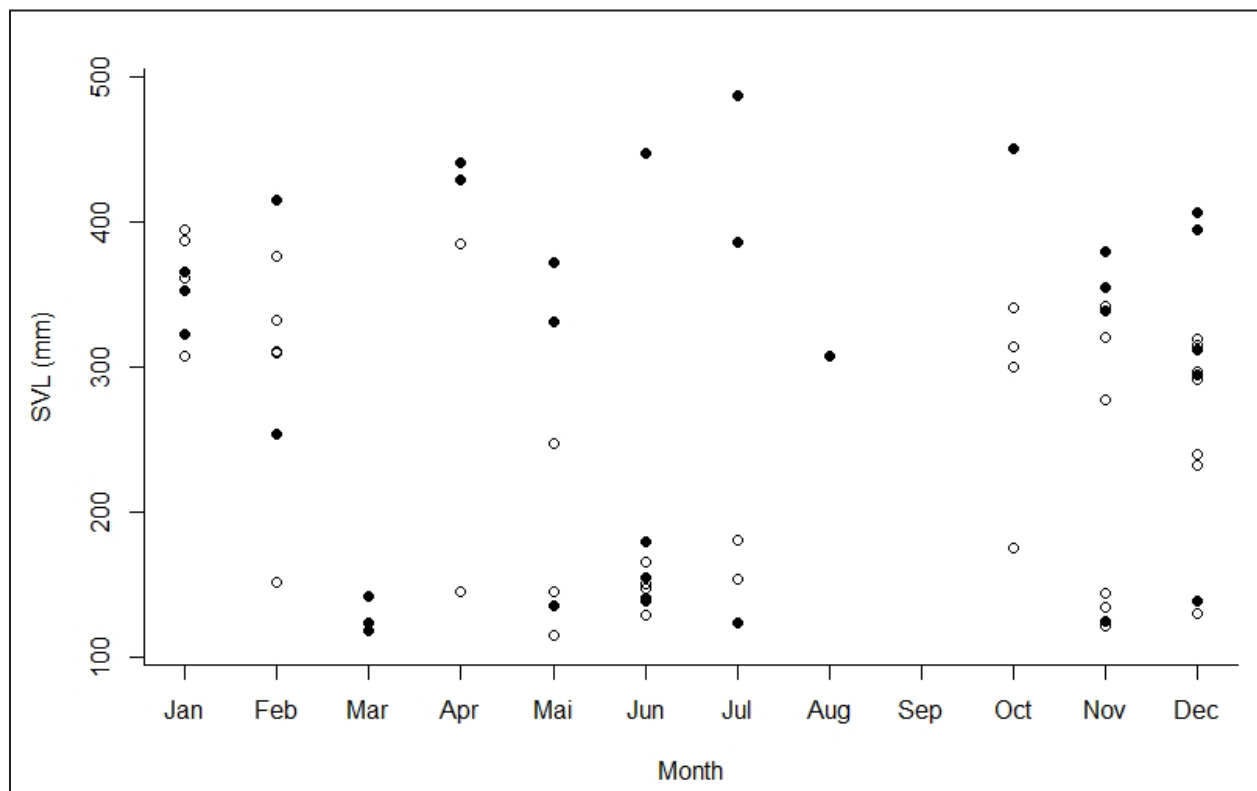


Figure 6. Temporal variation of snout-vent length of males (white dots) and females (black dots) of *X. matogrossensis*.

or eggs at the same time can also be sometimes observed when females are ready to receive the follicles that were not ovulated (Almeida Santos *et al.* 2014), what require that more studies need be done to confirm our hypothesis of multiple reproductive events in *X. matogrossensis*. Sexual dimorphism in body size, as observed in *X. matogrossensis*, is commonly found in other terrestrial snakes. The tail of males accommodates the hemipenes and their associated muscles, what results in longer tail and larger number of subcaudal scales when compared with females (King, 1989). Additionally, despite females usually being bigger than males because of enhanced fecundity (Seigel and Fitch, 1984; Shine, 1993; 1994), female body size does not explain the variation in the number of follicles and eggs in *X. matogrossensis*. Considering that more than 90% of the mature females measured around 300 mm or more of SVL (Fig. 3), we believe that at this size females of *X. matogrossensis* could be considered as reproductively actives. Also, early maturation imposes a higher cost on females (Madsen and Shine, 1994) and in many species of snakes the immature eggs or early developing follicles will not be recruited and, thus, will not fully develop into eggs (Seigel and Ford, 1987).

The information on the natural history of *X. matogrossensis* provided here, associated with the information on distribution and habitat use available in the literature (Nogueira *et al.*, 2019), can contribute to the assessment of the conservation status of this species and even to design conservation actions in case they are needed in the future.

Acknowledgements

We would like to thank Gustavo Graciolli (ZUFMS) for allowing us to review specimens under their care and Universidade Federal de Mato Grosso do Sul. HC would like to thank the Consejo Nacional de Ciencia y Tecnología (CONACYT), for partial financial support through the Programa Nacional de Incentivo a Investigadores (PRONII), and Coordenação de Aperfeiçoamento Pessoal de Nível Superior (CAPES, Brazil), Programa de Estudantes-Convênio de Pós-graduação (PEC-PG), for a fellowship. MM thanks Fundação de Amparo à Pesquisa do Estado de São Paulo for a grant (# 2018/14091-1) and CNPq for a research fellowship (# 306961/2015-6). This study was partially funded by CAPES/ Brazil - Finance Code 001 and Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia do Estado de Mato Grosso do Sul (# 187/2014). Conselho Na-

cional de Desenvolvimento Científico e Tecnológico (CNPq) provided a researcher's fellowship to VLF (PQ2/CNPq #309305/2018-7) and partial financial support to project (CNPq #409003/2018-2).

Literature cited

- Almeida-Santos, S.M. & Salomão, M.G. 2002. Reproduction in neotropical pitvipers, with emphasis on species of the genus *Bothrops*: 445-462. In: Schuett, G.W., Höggren, M., Douglas, M.E. & Greene, H.W. (eds.), *Biology of the Vipers*. Eagle Mountain Publishing, Carmel.
- Almeida-Santos, S.M.; Braz, H.; Santos, L.; Sueiro, L.; Barros, V.; Rojas, C. & Kasperovicz, K. 2014. Biología reproductiva de serpientes: recomendaciones para a coleta e análise de dados. *Herpetologia Brasileira* 3: 14-24.
- Andrews, R.M. & Mathies, T. 2000. Natural history of reptilian development: constraints on the evolution of viviparity. *BioScience* 50: 227-238.
- Ávila, R.W.; Ferreira, V.L. & Arruda, J.A.O. 2006. Natural History of the South American Water Snake *Helicops leopardinus* (Colubridae: Hydrophini) in the Pantanal, Central Brazil. *Journal of Herpetology* 40: 274-279.
- Ávila, R.W.; Kawashita-Ribeiro, R.A.; Ferreira, V.L. & Strüssmann, C. 2010. Natural history of the coral snake *Micrurus pyrrhocryptus* Cope 1862 (Elapidae) from semideciduous forests of western Brazil. *South American Journal of Herpetology* 5: 97-101.
- Blackburn, D.G. 1998. Structure, function and evolution of the oviducts of squamate reptiles, with special reference to viviparity and placentation. *The Journal of Experimental Zoology* 282: 560-617.
- Cabral, H.; Piatti, L.; Souza, F.; Scrocchi, G. & Ferreira, V. 2015. *Xenodon pulcher* (Jan, 1863) (Serpentes: Dipsadidae) first record for Brazil and a distribution extension. *Herpetology Notes* 8: 361-364.
- Carreira, S. 2002. Alimentación de los ofidios de Uruguay. *Asociación Española de Herpetología. Monografías de Herpetología* 6: 1-129.
- Carreira, S. & Lombardo, I. 2007. *Lystrophis histricus* (Rayed or Jan's Hog-nosed Snake). Diet. *Herpetological Review* 38: 208.
- Cei, J. 1993. Reptiles de noroeste, nordeste y este de la Argentina; Herpetofauna de las selvas subtropicales, Puna y Pampas. *Museo Regionale di Scienze Naturali di Torin* 14: 1-949.
- Eisfeld, A. & Vrcibradic, D. 2019. Reproductive aspects of the semi-aquatic snake *Erythrolamprus miliaris* (Dipsadidae: Xenodontini) in the state of Rio de Janeiro, southeastern Brazil. *Anais da Academia Brasileira de Ciências* 91: e20170657. doi.org/10.1590/0001-3765201920170657.
- Gibbons, J.W. & Lovich, J.E. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetological Monographs* 1990: 1-29.
- Giraud, A. 1997. Geographic Distribution. *Lystrophis matogrossensis*. *Herpetological Review* 28: 159.
- Giraud, A. 2002. Serpientes de la Selva Paranaense y del Chaco Húmedo. Literature of Latin America. Monografía 17, Buenos Aires.
- Gregory, P.T.; Crampton, L.H. & Skebo, K.M. 1999. Conflict and interactions among reproduction, thermoregulation, and feeding in viviparous reptiles: are gravid snakes anorexic? *Journal of Zoology* 248: 231-241
- Gudynas, E. 1979. Notes on the ecology of *Lystrophis dorbignyi* in Uruguay. *ASRA Journal* 1: 24-33.
- King, R. 1989. Sexual dimorphism in snakes tail length: sexual selection, natural selection, or morphological constraint? *Biological Journal of the Linnean Society* 38: 133-154.
- Lema, T.; Araujo, M.L. & Azevedo, A.C.P. 1983. Contribuição ao conhecimento da alimentação e do modo alimentar de serpentes do Brasil. *Comunicações do Museu de Ciências da PUC-RS* 26: 41-121.
- Madsen, T. & Shine, R. 1994. Costs of reproduction influence the evolution of sexual size dimorphism in snakes. *Evolution* 48: 1389-1397.
- Mesquita, P.C.; Sá-Polidoro, G.L. & Cechin, S.Z. 2013. Reproductive biology of *Philodryas olfersii* (Serpentes, Dipsadidae) in a subtropical region of Brazil. *Herpetological Journal* 23: 39-44.
- Monteiro, C.; Montgomery, C.; Spina, F.; Sawaja, R. & Martins, M. 2006. Feeding, Reproduction, and Morphology of *Bothrops matogrossensis* (Serpentes, Viperidae, Crotalinae) in the Brazilian Pantanal. *Journal of Herpetology* 40: 408-413.
- Nenda, S.J. & Cacivio, P.M. 2007. Reptilia, Colubridae, Xenodontinae, *Lystrophis dorbignyi*, *Lystrophis pulcher*, and *Lystrophis semicinctus*: Distribution extension, new provinces records in Argentina. *Check List* 3:126-130
- Nogueira, C.C.; Argôlo, A.J.S.; Arzamendia, V.; Azevedo, J.A.; Barbo, F.E.; Bérnils, R.S.; Bolocho, B.E.; Borges-Martins, M.; Brasil-Godinho, M.; Braz, H.; Buononato, M.A.; Cisneros-Heredia, D.F.; Colli, G.R.; Costa, H.C.; Franco, F.L.; Giraud, A.; Gonzalez, R.C.; Guedes, T.; Hoogmoed, M.S.; Marques, O.A.V.; Montingelli, G.G.; Passos, P.; Prudente, A.L.C.; Rivas, G.A.; Sanchez, P.M.; Serrano, F.C.; Silva Jr, N.J.; Strüssmann, C.; Vieira-Alencar, J.P.S.; Zaher, H.; Sawaya, R.J. & Martins, M. 2019. Atlas of Brazilian Snakes: Verified Point-Localities Maps to Mitigate the Wallacean Shortfall in a Megadiverse Snake Fauna. *South American Journal of Herpetology* 14(sp1): 1-274.
- Oksanen, J.; Blanchet, F.G.; Friendly, M.; Kindt, R.; Legendre, P.; McGlenn, D.; Minchin, R.P.; O'Hara, R.B.; Simpson, G.; Solymos, P.; Henry, M.; Stevens, H.; Szoecs, E. & Wagner, H. 2013. vegan: Community Ecology Package. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>
- Oliveira, M. E. & Martins, M. 2002. When and where to find a pitviper: activity patterns and habitat use of the lancehead, *Bothrops atrox*, in central Amazonia, Brazil. *Herpetological Natural History* 8: 101-110.
- Oliveira, R.B.; Di-Bernardo, M.; Funk Pontes, G.M.; Macieland, A.P. & Krause, L. 2001. Dieta e comportamento alimentar da cobra nariguda, *Lystrophis dorbignyi* (Duméril, Bibron & Duméril, 1854), no litoral norte do Rio Grande do Sul, Brasil. *Cuadernos de Herpetología* 14: 117-122.
- Oliveira, R.B.; Funk-Pontes, G.M.; Maciel, A.P.; Gomes, L.R. & Di-Bernardo, M. 2011. Reproduction of *Xenodon dorbignyi* on the north coast of Rio Grande do Sul, Brazil. *Herpetological Journal* 21: 219-225.
- Orejas-Miranda, B.R. 1966. The Snake *Lystrophis* in Uruguay. *Copeia* 1966: 193-205.
- Pinto, R.R. & Fernandes, R. 2004. Reproductive biology and diet of *Liophis poecilopyrus poecilopyrus* (Serpentes, Colubridae) from southeastern Brazil. *Phyllomedusa* 3: 9-14.
- Pizzatto, L. & Marques, OAV. 2002. Reproductive biology of the false coral snake *Oxyrhopus guibeii* (Colubridae) from southeastern Brazil. *Amphibia-Reptilia* 23: 495-504.
- Pizzatto, L. & Marques, OAV. 2006. Interpopulational variation

- in reproductive cycles and activity of the water snake *Liophis miliaris* (Colubridae) in Brazil. *Herpetological Journal* 16: 353-362.
- Pizzatto L.; Jordão R.S. & Marques O.A.V. 2008. Overview of reproductive strategies in Xenodontini (Serpentes: Colubridae: Xenodontinae) with new data for *Xenodon neuwiedii* and *Waglerophis merremii*. *Journal of Herpetology* 42: 153-162.
- Pleguezuelos, J. & Fahd, S. 2004. Body size, diet and reproductive ecology of *Coluber hippocrepis* in the Rif (Northern Morocco). *Amphibia-Reptilia* 25: 287-302
- Prado, C., Uetanabaro, M. & Haddad, C. 2005. Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. *Amphibia-Reptilia* 26: 211-221.
- R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Sawaya, R. J.; Marques, O. A. V. & Martins, M. 2008. Composição e história natural das serpentes de Cerrado de Itirapina, São Paulo, sudeste do Brasil. *Biota Neotropica* 8: 127-149.
- Seigel, R. & Fitch, H. 1984. Ecological patterns of relative clutch mass in snakes. *Oecologia* 61: 293-301.
- Seigel, R.A. & Ford, N.B. 1987. Reproductive ecology. 210- 252. *In: Seigel, R.A., Collins, J.T. & Novak, S.S. (eds), Snakes: Ecology and Evolutionary Biology.* New York: McMillan Publishing Company.
- Scrocchi, G. & Cruz, F. 1993. Description of a new species of genus *Lystrophis* Cope and a revalidation of *Lystrophis pulcher* (Jan, 1863) (Serpentes; Colubridae). *Papéis Avulsos de Zoologia* 38: 171-186.
- Shine, R. 1980. "Costs" of reproduction in reptiles. *Oecologia* 46: 92-100.
- Shine, R. 1982. Ecology of the Australian elapid snake *Echiopsis curta*. *Journal of Herpetology* 16: 388-393
- Shine, R. 1985. The evolution of viviparity in reptiles: an ecological analysis: 605-694. *In: Gans, C. & Billett, F. (eds.), Biology of the Reptilia, Volume 15.* John Wiley and Sons. New York, N.Y.
- Shine, R. 1993: Sexual dimorphism in snakes: 49-86. *In: Snakes: Ecology & Behavior*, Seigel, R.A. & Collins, J.T., (eds), New York. McGraw-Hill, Inc.
- Shine, R. 1994. Sexual size dimorphism in snakes revisited. *Copeia* 1994: 326-346.
- Shine, R. 2003. Reproductive strategies in snakes. *Proceedings of the Royal Society of Biological Sciences* 270: 995-1004.
- Strüssmann, C., Prado, C.; Ferreira, V. & Kawashita-Ribeiro, R.A. 2011. Diversity, ecology, management and conservation of amphibians and reptiles of the Brazilian Pantanal: a review. 497-521. *In: Junk, W.L.; Silva, C.J.; Nunes da Cunha, C. & Wantzen, K.M. (eds.), The Pantanal – Ecology, biodiversity and sustainable management of large neotropical seasonal wetland.* Pensoft Publishers. Sofia.
- Williams, J.D. & Scrocchi, G.J. 1994. Ofidios de agua dulce de la República Argentina. *Fauna de agua dulce de la República Argentina* 42: 1-55.
- Zaher, H.; Grazziotin, F.G, Cadle, J.E.; Murphy, G.W.; Moura-Leite, J.C. & Bonatto, S.L. 2009. Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American Xenodontines: A revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia* (São Paulo) 49: 115-153.

Appendix I

Specimens examined

Xenodon matogrossensis: (BRAZIL): *Mato Grosso do Sul*: Anastácio - ZUFMSREP 01463, ZUFMSREP 01523, ZUFMSREP 01650, ZUFMSREP 01654; Aquidauana - ZUFMSREP 00091, ZUFMSREP 00108, ZUFMSREP 0250, ZUFMSREP 0540, ZUFMSREP 0541, ZUFMSREP 0543, ZUFMSREP 0545, ZUFMSREP 0546, ZUFMSREP 0547, ZUFMSREP 0606, ZUFMSREP 0607, ZUFMSREP 0608, ZUFMSREP 0612, ZUFMSREP 01464, ZUFMSREP 01465, ZUFMSREP 01466, ZUFMSREP 01467, ZUFMSREP 01468, ZUFMSREP 01470, ZUFMSREP 01471, ZUFMSREP 01472, ZUFMSREP 01473, ZUFMSREP 01474, ZUFMSREP 01475, ZUFMSREP 01512, ZUFMSREP 01537, ZUFMSREP 01570, ZUFMSREP 01604, ZUFMSREP 01620, ZUFMSREP 01631, ZUFMSREP 01648, ZUFMSREP 01660, ZUFMSREP 01690, ZUFMSREP 01694, ZUFMSREP 01700, ZUFMSREP 01701, ZUFMSREP 01720, ZUFMSREP 01955, ZUFMSREP 01983, ZUFMSREP 01984, ZUFMSREP 01986, ZUFMSREP 01987, ZUFMSREP 01988, ZUFMSREP 01989, ZUFMSREP 01990, ZUFMSREP 01991, ZUFMSREP 01992, ZUFMSREP 01993, ZUFMSREP 01994, ZUFMSREP 01996, ZUFMSREP 01997, ZUFMSREP 01998, ZUFMSREP 01999, ZUFMSREP 02001, ZUFMSREP 02002, ZUFMSREP 02003, ZUFMSREP 02004, ZUFMSREP 02145, ZUFMSREP 03539; Bodoquena: ZUFMSREP 01995; Corumbá: ZUFMSREP 01291, ZUFMSREP 03542, ZUFMSREP 03540, ZUFMSREP 03541; Miranda: ZUFMSREP 02153; Porto Murtinho: ZUFMSREP 0604, ZUFMSREP 0609, ZUFMSREP 02755.