Journal of Herpetology, Vol. 40, No. 3, pp. 408–413, 2006

Feeding, Reproduction, and Morphology of *Bothrops mattogrossensis* (Serpentes, Viperidae, Crotalinae) in the Brazilian Pantanal

Carolina Monteiro,[1,2] Chad E. Montgomery,[3] Felipe Spina,[1] Ricardo J. Sawaya,[4] and Marcio Martins[1]

[1]*Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, 05508-090 São Paulo, São Paulo, Brazil*
[3]*Biology Department, 1725 State Street, University of Wisconsin-La Crosse, 54601, La Crosse, Wisconsin, USA*
[4]*Laboratório de Herpetologia, Instituto Butantan. Avenida Dr. Vital Brazil, 1500, 05503-900 São Paulo, São Paulo, Brazil*

Abstract.—*Bothrops mattogrossensis* occurs in open wet habitats in the Pantanal of western Brazil. As part of a series of studies focusing on how ecological characters evolved in the genus *Bothrops*, we gathered information on diet, reproduction, and morphology for *B. mattogrossensis* using museum specimens. *Bothrops mattogrossensis* has a generalized diet (anurans, small mammals, lizards, snakes, and centipedes), a plesiomorphic character in the genus *Bothrops*. We found no evidence of an ontogenetic shift in diet from ectothermic to endothermic prey, as observed in other species of *Bothrops*. Feeding frequency is high (68.8%) compared to other *Bothrops* spp. Reproduction is seasonal, with a vitellogenic period concentrated at the end of the dry season. Fecundity is relatively high, with clutch size varying from 18–37. Females are significantly larger in snout–vent length and have significantly shorter tails and relatively larger heads than males. Although mostly terrestrial, *B. mattogrossensis* is relatively slender and has a longer tail than other terrestrial *Bothrops*, possibly an adaptation for climbing into vegetation during seasonal floods.

Recent studies have resulted in the accumulation of information on the natural history of several species of *Bothrops* (e.g., , 2002; Valdujo et al., 2002; Nogueira et al., 2003; Campbell and Lamar, 2004). General patterns have emerged from these studies:(1) Most species are generalists and have an ontogenetic shift in diet (from ectothermic to endothermic prey); (2) A generalist diet reflects the availability of prey in the habitat; (3) Arboreal species of *Bothrops* have significantly longer tails and are more slender than terrestrial forms (Martins et al., 2001, 2002).

The genus *Bothrops* represents a recent radiation of pitvipers with 30 terrestrial species, distributed from Mexico to Argentina (Greene, 1992; Salomão et al., 1997; Wüster et al., 2002; Campbell and Lamar, 2004). Species of *Bothrops* occupy a diversity of habitats, ranging from forested to open areas (Martins et al., 2002). When *Bothriopsis* is considered a synonym of *Bothrops* (see Wüster et al., 2002), the genus includes primarily terrestrial, semiarboreal, and almost completely arboreal species (Martins et al., 2001). The *Bothrops neuwiedi* complex is widespread in South America (Silva, 2004) and is considered primarily terrestrial (Martins et al., 2001). This complex encompasses seven species, which shows relatively high biological diversity. They occur in grasslands (e.g., *Bothrops neuwiedi*), savannas (e.g., *Bothrops pauloensis, Bothrops lutzi*), and even forests (e.g., *Bothrops pubescens*) and feed primarily on mammals, lizards, and frogs (Campbell and Lamar, 2004; Martins et al, 2002; Valdujo et al., 2002; Hartmann et al., 2004). Species associated with wetter habitats like *B. pubescens* feed more frequently on frogs than on lizards, whereas the opposite was observed in species that inhabit drier habitats, like *B. pauloensis*. Within *Bothrops*, the *B. neuwiedi* species group seems to form a monophyletic clade with the *B. jararaca* group (Wüster et al., 2002), characterized by semiarboreal forest species (Campbell and Lamar, 2004).

The *B. neuwiedi* complex formerly included 12 subspecies ranging from southern to northeastern Brazil (Campbell and Lamar, 1989), but recently the complex was divided into seven full species (Silva, 2004). In a recent taxonomic study based on morphology, Silva (2004) considered the previous subspecies *B. neuwiedi mattogrossensis* (Mato Grosso Lancehead) as *B. mattogrossensis*. The Mato Grosso Lancehead is distributed in wet flooded areas of the Pantanal region of western Brazil, and it also occurs in Peru (Sandia region), Bolivia, Paraguay, northern Argentina, and other Brazilian States including Amazonas (isolated population in the fields of Humaitá), Rondônia, Mato Grosso do Sul, Tocantins, Goiás, and São Paulo (from approximately 7° to 24°S latitude; Silva, 2004).

As part of a series of studies aiming to explore how ecological characters evolved in pitvipers of the genus *Bothrops* (e.g., Martins et al., 2002; Valdujo et al., 2002; Nogueira et al., 2003; Hartmann et al., 2004), we gathered information on diet, reproduction, and morphology for *B. mattogrossensis* using museum specimens. Because this species lives in seasonably floodable habitats, we expected to find differences in its ecology in relation to other species of the *B. neuwiedi* complex that inhabit flooded habitats. We predicted that these differences would reflect selective agents related to the dynamic habitat of *B. mattogrossensis*.

Materials and Methods

We examined 93 preserved specimens of *B. mattogrossensis* from the herpetological collection of the Instituto Butantan (IB; see Appendix 1). All specimens were collected in Mato Grosso and Mato Grosso do Sul states, western Brazil. Our sample included specimens of all size classes, chosen independently of the presence of palpable food items. Only individ-

---

[2] Corresponding Author. Department of Biological Sciences, 632 Science Engineering, University of Arkansas, Fayetteville, Arkansas 72701, USA; E-mail: karol_monteiro@yahoo.com

TABLE 1. Character loadings, eigenvalues, and the percentage of total variance explained for the first two principal components (PC1, PC2) among five morphological characters of adult males (N = 38) and females (N = 40) of *Bothrops mattogrossensis*. Characters: snout–vent length (SVL); tail length (TAIL); head width (HW); head length (HL); and body mass (MASS).

	PC1	PC2
SVL	0.46	−0.09
TAIL	0.41	0.85
HW	0.44	−0.47
HL	0.46	−0.18
MASS	0.44	−0.04
Eigenvalue	4.43	0.3
Var (%)	88.7	6.05

uals that were wild-caught and preserved soon after collecting were included.

The following morphological data were recorded for each specimen: snout–vent length (SVL), head length (HL), head width (HW), tail length (TAIL), and wet body mass (to nearest gram, after draining excess of preservative, cf. Martins et al., 2001). These five morphological characters were chosen because they are all indications of overall body size and body shape. We also recorded the following data when possible: prey type in gut (identified as anurans, small mammals, lizards, snakes, or centipedes), sex and reproductive maturity, number of enlarged ovarian follicles (> 5 mm; cf. Shine, 1980), diameter of largest ovarian follicles or encapsulated oviductal embryos, diameter of testes, and diameter of larger ductus deferentia near cloaca.

We tested for ontogenetic shift in prey type (ectotherms and endotherms) by comparing the frequency of prey types in juveniles and adults with a Fisher exact test. We also tested for ontogenetic shift in prey type by comparing the SVL of snakes that consumed ectothermic and endothermic prey with a Mann-Whiney *U*-test (e.g., Martins et al., 2002). All diet statistical analyses were performed using Statistica (Release 5.1J, StatSoft, Tulsa, OK, 1998), and a significance level of $\alpha = 0.05$ was assumed for all analyses.

We classified females as reproductive if they were gravid or had ovarian follicles > 5 mm (cf. Shine, 1980). The female reproductive cycle was determined by the number and size of vitellogenic ovarian follicles or oviductal embryos. The male reproductive cycle was quantified by diameter of testes and right deferent duct. Males were considered mature if they had enlarged testes or opaque and twisted deferent ducts (cf. Shine, 1980; Marques, 1996a,b).

We performed principal components analysis (PCA; Johnson, 1998; Montgomery et al., 2003) on the correlation matrix of five morphological variables to create simple linear combinations that explain the variance in the morphological data set (Johnson, 1998; Montgomery et al., 2003). We used only principal components PC1 and PC2 in the analysis because together they accounted for 94.7% of the total variance. All five morphological variables were equally positively weighted in PC1; therefore, PC1 was interpreted as a size indicator whereas PC2 indicated shape (Table 1). In PC2, tail length was highly positively weighted, whereas head length and head width were negatively weighted, indicating an inverse relationship between the head characters and TAIL (Table 1).

To test for sexual size dimorphism (SSD), we used one-way analysis of variance (ANOVA) to test for significant differences in the first principal component scores between the sexes. We also used ANOVA to compare the second principal component scores between the sexes to determine whether the inverse relationships of the head characters and TAIL were caused by sexual dimorphism. We used analysis of covariance (ANCOVA) with the general model (LogY = LogSVL + SEX + LogSVL · SEX; where Y = MASS, HL, HW, or TAIL), using sex as an independent variable, to examine the relationships of these four characters between the sexes. All morphological variables were log-transformed prior to ANCOVA to linearize the relationships. There was no significant interaction between LogSVL and SEX for each of the response variable; thus, meeting the assumption of homogeneous slopes (ANCOVA: LogMASS: $F_{1,74} = 0.42$, $P = 0.51$; LogHL: $F_{1,73} = 2.08$, $P = 0.15$; LogHW: $F_{1,74} = 0.05$, $P = 0.05$; LogTAIL: $F_{1,72} = 0.01$, $P = 0.92$. We used JMP® 3.22 (SAS Institute, Cary, NC, 1997) for all morphological statistical analyses.

RESULTS

Diet.—In 93 individuals, we found 51 with prey items (feeding frequency = 54.8%; Table 2). Most of the prey items were found in the intestine (91.2%); 5.2% of examined prey was in the stomach or in the entire gut (3.5%). Only 12.2% of the snakes had more than one prey item in their gut. Of the prey consumed, 54.7% were ectothermic, and 45.3% were endothermic. Prey type included anurans (46.9%), small mammals (45.3%), lizards (4.6%), snakes (1.6%), and centipedes (1.6%; Table 2). *Bothrops mattogrossensis* does not show an ontogenetic shift in diet. The frequency of ectothermic and endothermic prey items consumed by juveniles and adults did not differ

TABLE 2. Contribution of main groups of prey to the diet of juvenile and adult *Bothrops mattogrossensis*.

Age group	With prey	No. of prey	Anurans	Mammals	Lizards	Snakes	Centipedes
Juveniles N = 10	6 (60%)	7	4	3	0	0	0
Adults N = 83	47 (56.6%)	57	26	26	3	1	1
Males N = 45	23 (49.1%)	30	14	14	1	0	1
Females N = 47	24 (50.8%)	27	12	12	2	1	0
Total N = 93	51 (54.8%)	64	30	29	3	1	1

significantly (Fisher exact test, $P = 0.61$; Table 2). The SVL of snakes that consumed ectothermic (median = 633 mm, range = 277–1072 mm, $N = 34$) and endothermic (median = 615 mm, range = 332–1072 mm, $N = 29$) prey did not differ significantly ($U = 456.00$, $P = 0.61$).

Reproduction.—We collected reproductive data on 49 females and 42 males. The smallest reproductive male in our sample was 410 mm in SVL, and the smallest reproductive female was 568 mm SVL. The female reproductive cycle is seasonal, with vitellogenic period concentrated at the end of the dry season. Females had vitellogenic follicles (> 5 mm) throughout the year; however, the largest follicles (25–30 mm) were found only at the end of the dry season, August to October (Fig. 1). Parturition occurs during the rainy season, October to December (Fig. 1), and clutch size varied from 18–37 ($N = 3$). The smallest snake measured was 236 mm SVL (caught in June; IB4839), and the largest embryo was 200 mm SVL (inside a gravid female caught in December; 1177 mm SVL; IB10245).

Mean deferent duct diameter was 0.84 ± 0.46 mm (range 0.05–1.82 mm), and the average testis diameter was 14.01 ± 6.53 mm (range 1.6–32.9 mm). Deferent duct and testis diameter varied temporally with the largest measurements occurring between March and June during the transition between wet and dry seasons (Fig. 2).

Morphology.—We included 78 mature individuals of *B. mattogrossensis* in our morphometric analysis (39 females and 38 males). Average adult female SVL was 794 ± 183 mm (range 568–1285 mm), and average adult male SVL was 579 ± 100 mm (range 410–833 mm).

The first principal component (PC1) accounted for 88.7% of the variation in the morphological variables (Table 1). Females were significantly larger than males (ANOVA on PC1 scores, $FT_{1,73} = 30.99$, $P < 0.0001$). The second principal component (PC2) accounted for 6.06% of the variation (Table 1). Males had significantly greater PC2 scores than females (ANOVA $F_{1,73} = 28.05$, $P < 0.0001$). Based on the PC2 scores, males had relatively longer tails and relatively shorter and narrower heads than did females. There was a significant difference in the relationship between LogTAIL and LogSVL between males and females (ANCOVA, $F_{1.73} = 40.65$, $P < 0.0001$), with males having relatively longer tails. There was also a significant difference in the relationship between LogHL and LogSVL (ANCOVA, $F_{1,74} = 9.67$, $P = 0.002$), and in the relationship between LogHW and LogSVL (ANCOVA, $F_{1.75} = 5.23$, $P = 0.02$) between males and females, with females having relatively longer and wider heads than males.

DISCUSSION

Bothrops mattogrossensis feeds on both ectothermic and endothermic prey items (small mammals, anurans, lizards, snakes, and centipedes). No prey type accounted for more than 50% of the total prey items found, which supports a previous report that the Mato Grosso lancehead is a generalist predator (Martins et al., 2002). Generalized diet seems to be a plesiomorphic character in the genus *Bothrops* (Greene, 1992; Sazima, 1992; Martins et al., 2002). Compared to the other species of the *B. neuwiedi* complex (e.g., Martins et al., 2002; Valdujo et al., 2002; Hartmann et al., 2004), *B. mattogrossensis* feeds very frequently on frogs and rarely on lizards, what may reflect its floodable habitat, where bodies of water are very abundant.

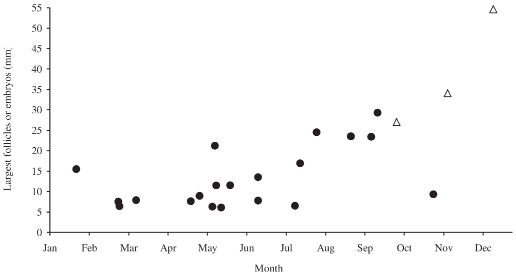

FIG. 1. Seasonal variation in the diameter of the largest vitellogenic follicle (dots), and encapsulated oviductal embryos (triangles) of 49 adult female *Bothrops mattogrossensis*. Dry season starts in mid-March and ends in mid-September, when the wet season (spring and summer) starts.

The Mato Grosso Lancehead does not appear to exhibit an ontogenetic diet shift, another apparently plesiomorphic character within *Bothrops* (Martins et al., 2002; Table 3). This lack of ontogenetic shift in diet in small species of *Bothrops* may reflect the fact that small adults of *Bothrops* still feed on ectotherms while beginning to feed on endotherms (Martins et al., 2002). Feeding frequency in our study was higher than reports for other *Bothrops* species (Martins et al., 2002; Table 3). A higher feeding frequency could reflect higher prey availability in the habitat of *B. mattogrossensis* (especially anurans). *Bothrops mattogrossensis* feeds more frequently on anurans than most other *Bothrops* (see Martins et al., 2002).

Reproduction is seasonal with the vitellogenic period concentrated during the rainy season, a character that is widespread in the *B. neuwiedi* complex and in *Bothrops* in general (Sazima, 1992; Almeida-Santos and Salomão, 2002; Valdujo et al., 2002; Hartmann et al., 2004). Parturition occurs during the rainy season, supporting a previous study (see Almeida-Santos and Salomão, 2002). Larger testicular and deferent duct sizes indicate that males are reproductive during the dry season, from March to

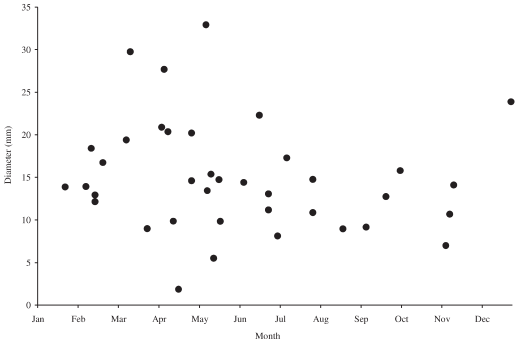

FIG. 2. Seasonal variation in the testis diameter of 42 adult males of *Bothrops mattogrossensis*.

TABLE 3. Relationship between ecological and morphological traits in the *Bothrops jararaca* and *Bothrops neuwiedi* groups. CS = clutch size; SD = sexual dimorphism in SVL; ♂ = male; ♀ = female; Arb = arboreality; OS = ontogenetic shift in diet; FF = feeding frequency; Gen = generalist; Y = present; N = absent. This summary is gleaned from the literature and from on going studies (Hoge et al., 1959; Sazima, 1992; Martins et al., 2001, 2002; Valdujo et al., 2002; Hartmann et al., 2004; F. Spina, unpubl. data; M. Martins, unpubl. data).

Species	CS	SD	Arb	OS	FF	Gen
B. mattogrossensis	18–37	♀larger HL & SVL ♂larger TAIL	Y	N	68.8	Y
B. neuwiedi	14–16	♀larger HL ♂larger TAIL	N	N	40.9	N
B. pauloensis	4–20	♀>SVL & mass ♂larger TAIL	N	Y	35.0	Y
B. pubescens	4–25	♀>SVL & mass ♂larger TAIL	N	N	32.0	Y
B. erytromelas	?	♀SVL = ♂SVL ♀mass = ♂mass ♂larger TAIL	N?	N?	?	Y
B. jararaca	3–34	♀>SVL & mass ♂larger TAIL	Y	Y	29.0	Y
B. insularis	3–10	♀>SVL & mass ♂larger TAIL	Y	Y	?	Y

June (Shine, 1977, Almeida-Santos and Salomão, 2002). The interval between copulation and vitellogenesis could be caused by morphological changes in females that occur after copulation (e.g., uterine muscular twisting, c.f. Almeida-Santos and Salomão, 2002; Hartmann et al., 2004), suggesting the occurrence of sperm storage in these snakes. Species of the *B. neuwiedi* group complex are known to produce neonates of small size and to display low fecundity caused by their relatively small body size (Valdujo et al., 2002; Hartmann et al., 2004).

Bothrops mattogrossensis is sexually dimorphic with females having relatively larger heads and longer bodies, and males having relatively longer tails, as in other *Bothrops*. The difference in relative tail size between males and females is most probably a result of morphological constraints of the hemipenes and its retractor muscles (Shine, 1993). Larger body size of females may be a result of size-dependent fecundity, providing more space for reproductive organs and embryos within the body cavity (Shine, 1993). Larger heads in females are a possible adaptation for ingesting larger prey items (Pough and Groves, 1983; Shetty and Shine, 2002). Larger relative female head length has been demonstrated in the *B. neuwiedi* complex, and the occurrence of larger female head length within the complex may reflect sexual differences in diet (Martins et al., 2002; Valdujo et al., 2002; Hartmann et al., 2004). We found no evidence of sexual difference in the diet of *B. mattogrossensis*; however, sexes may differ in the relative size of prey. Alternatively, sexual dimorphism in head morphology observed for the Mato Grosso Lancehead may be a result of a phylogenetic effect, as other members of the complex possess head dimorphism (see Martins et al., 2002; Valdujo et al., 2002; Hartmann et al., 2004).

The Pantanal region has two seasons: a wet season (October to March) during which the region is flooded as a consequence of the overflowing of its numerous waterways, and a dry season (April to September; Junk and Silva, 1995). As a result of the topography and the seasonal climate, the landscapes consist of swamps, seasonally flooded grass lands and woodlands, and various types of forest (evergreen, semideciduous, riparian; Junk and Silva, 1995). The Mato Grosso Lancehead is partially arboreal and is commonly found in wet flooded areas of the Pantanal region of western Brazil. But basic ecological attributes of *B. mattogrossensis* such as habitat use and activity are still poorly known (Strüssmann and Sazima, 1993). Terrestrial lifestyles are widespread in *Bothrops* and have been proposed as the plesiomorphic state for the genus (Martins et al., 2001). Relatively shorter tail length is correlated with a terrestrial lifestyle (Martins et al., 2001). Although apparently terrestrial, the Mato Grosso Lancehead seems to have a relatively more slender body and longer tail than other species in the *B. neuwiedi* group (cf. Martins et al., 2001), suggesting a trend toward more arboreal activity. But more information on natural history is needed to test this hypothesis. This species may be forced to adopt an arboreal lifestyle during seasonal flooding (Strüssmann and Sazima, 1993), which could be a selective force for a more slender body form and a longer tail (Martins et al., 2001).

Acknowledgments.—We thank M. T. Almeida, S. Almeida-Santos, O. A. V. Marques, and C. Nogueira for providing assistance and unpublished data and Instituto Butantan (F. L. Franco and V. J. Germano), which made possible analysis of specimens. We are grateful to S. J. Beaupre, H. W. Greene, N. E. Haertle, M. Pilgrim, R. Wittenberg, K. Zamudio, and two anonymous reviewers who critically read the manuscript; Idea Wild (Biodiversity Conservation Organization) for donating equipment. This work is part of the *Bothrops* Natural History and Evolution Project funded by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP; 95/09642-5 and 00/12339-2). FAPESP also provided fellowship to CM (01/03516-0). MM thanks CNPq (Brazilian Research Council) for a providential fellowship.

Literature Cited

Almeida-Santos, S., and M. Salomão. 2002. Reproduction in neotropical pit vipers, with emphasis on species of the genus *Bothrops*. *In* G. W. Schuett, M. Höggren, and H. W. Greene (eds.), Biology of the Vipers, pp. 445–462. Eagle Mountain Publishing, Eagle Mountain, UT.

Campbell, J. A., and W. W. Lamar. 1989. The Venomous Reptiles of Latin America. Cornell University Press, Ithaca, NY.

———. 2004. The Venomous Reptiles of the Western Hemisphere. Cornell University Press, Ithaca, NY.

Greene, H. W. 1992. The ecological and behavioral context of pitviper evolution. *In* J. A. Campbell and E. D. Brodie (eds.), Biology of the Pitvipers, pp. 107–117. Selva, Tyler, TX.

———. 1994. Systematics and natural history, foundations for understanding and conserving biodiversity. American Zoologist 34:48–56.

Hartmann, M. T., O. A. V. Marques, and S. M. Almeida-Santos. 2004. Reproductive biology of the southern Brazilian pitviper *Bothrops neuwiedi pubecens* (Serpentes, Viperidae). Amphibia-Reptilia 25:77–85.

Hoge, A. R., H. E. Belluomini, G. Schreiber, and A. M. Penha. 1959. Sexual abnormalities in *Bothrops insularis* (Amaral) 1921. (Serpentes: Crotalinae). Memórias do Instituto Butantan 29:17–88.

Johnson, D. E. 1998. Applied Multivariate Methods for Data Analysis. Brooks/Cole Publishers Co., Pacific Grove, CA.

Junk, W. J., and C. J. da Silva. 1995. Neotropical floodplains: a comparison between the Pantanal of Mato Grosso and the large Amazonian river floodplains. *In* Limnology in Brazil. J. G. Tundisi, C. E. M. Bicudo, and T. Matsumura Tundisi (eds.), Brazilian Academy of Sciences and Brazilian Limnological Society, São Paulo, Brazil.

Marques, O. A. V. 1996a. Reproduction, seasonal activity and growth of the coral snake, *Micrurus corallinus* (Elapidae), in the southeastern Atlantic forest in Brazil. Amphibia-Reptilia 17:277–285.

———. 1996b. Biologia reprodutiva da cobra-coral *Erythrolamprus aescularpi* Linnaeus (Colubridae), no sudeste do Brasil. Revista brasileira de Zoologia 13:747–753.

Martins, M., M. S. Araújo, R. J. Sawaya, and R. Nunes. 2001. Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of Neotropical pitvipers (*Bothrops*). Journal of Zoology, London 254:529–538.

Martins, M., O. A. V. Marques, and I. Sazima. 2002. Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers of the genus *Bothrops*. *In* G. W. Schuett, M. Höggren, and H. W. Greene (eds.), Biology of the Vipers, pp. 307–328. Eagle Mountain Publishing, UT.

Montgomery, C. E., S. P. Mackessy, and J. C. Moore. 2003. Body size variation in the Texas Horned Lizard, *Phrynosoma cornutum*, from Central Mexico to Colorado. Journal of Herpetology 37:550–553.

Nogueira, C., R. J. Sawaya, and M. Martins. 2003. Ecology of the pitviper, *Bothrops moojeni*, in the Brazilian cerrado. Journal of Herpetology 37: 653–659.

Pough, F. H., and J. D. Groves. 1983. Specialization of the body form and food habits of snakes. American Zoologist 23:443–454.

Salomão, M. G., W. Wüster, R. S. Thorpe, J.-M. Touzet, and BBBSP. 1997. DNA evolution of South American pitvipers of the genus *Bothrops* (Reptilia: Serpentes: Viperidae). Symposium of Zoological Society, London 70:89–98.

Sazima, I. 1992. Natural history of the jararaca pitviper, *Bothrops jararaca*, in southeastern Brazil. *In* J. A. Campbell and E. D. Brodie (eds.), Biology of the Pitvipers-Selva, Tyler, TX.

Shetty, S., and R. Shine. 2002. Sexual divergence in diets and morphology in Fijian sea snakes *Laticauda colubrine* (Laticudinae). Austral Ecology 27:77–84.

Shine, R. 1977. Reproduction in Australian elapid snakes I. Testicular cycles and mating seasons. Australian Journal of Zoology 25:647–653.

———. 1980. Comparative ecology of three Australian snakes species of the genus *Cacophis* (Serpentes, Elapidae). Copeia 1980:831–838.

———. 1993. Sexual dimorphism in snakes. *In* Snakes: Ecology and Behavior., R. A. Seigel and J. T. Collins (eds.). McGraw-Hill, Inc. New York.

Shine, R., and N. Charles. 1982. Ecology of Australian elapid snake *Tropidechis carinatus*. Journal of Herpetology 16:383–387.

Silva, V. X. 2004. The *Bothrops neuwiedi* Complex. *In* J. A. Campbell and W. W. Lamar. The Venomous Reptiles of the Western Hemisphere, pp. 410–422. Cornell University Press, Ithaca, NY.

Strüssmann, C., and I. Sazima. 1993. The snake assemblage of the Pantanal at Poconé, western Brazil: faunal composition and ecological summary. Studies of Neotropical Fauna Environments 28: 157–168.

Valdujo, P. H., C. Nogueira, and M. Martins. 2002. Ecology of *Bothrops neuwiedi pauloensis* (Serpentes: Viperidae: Crotalinae) in the Cerrado of central and southeastern Brazil. Journal of Herpetology 36:169–176.

Wüster, W., M. G. Salomão, J. A. Quijada-Mascareñas, R. S. Thorpe, and BBBSP. 2002. Origin and evolution of South American pitviper fauna: evidence from mitochondrial DNA sequence analysis. *In* G. W. Schuett, M. Höggren, and H. W. Greene (eds.), Biology of the Vipers, pp. 111–128. Eagle Mountain Publishing, Eagle Mountain, UT.

Accepted: 12 June 2006.

Appendix 1

Material Examined.—All specimens numbers refers to holdings of the Instituto Butantan (IB).

Brazil: Mato Grosso do Sul: Aquidauana (4417, 5219, 5360, 6119, 6299, 11597, 11600, 11602, 11824, 11846, 11928, 13591, 13592, 16835, 16975, 16976, 17031, 18598, 18610, 18916, 19019, 19390, 19759, 19760, 19761, 19762, 20512, 20513, 29103, 32320, 33041, 33260, 33595).

Porto Murtinho (13821, 19764, 26173, 26174, 26720, 26721, 29746, 55675).

Mato Grosso: Caceres (22986, 23849, 24109, 24114, 24135), Colonia Indigena Sao Marcos (37578).

Corumba (5900, 6506, 10245, 11868, 12263, 19077, 55594).

Cuiaba (20885, 24634, 24635, 25049, 26008, 26144, 26145, 26146, 26326, 26327, 28040, 28041, 28042, 32745, 33217, 33319, 53516, 56641).

Enguia Lopez (15474).

Forte Coimbra (32850, 26457, 26719, 32853).

Guaicurus (12994).

Nhecolandia (5527, 5605, 6507, 6928, 7527, 8525).

Pantanal (24393).

Ponta Pora (13322, 55389).

Porto Esperanca (4839, 4858, 12548, 12609).

Sao Simao (56643, 56799).