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Natural History of *Bothrops itapetiningae* Boulenger, 1907 (Serpentes: Viperidae: Crotalinae), an Endemic Species of the Brazilian Cerrado

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ABSTRACT.—We present data on habitat use, activity, sexual dimorphism, reproduction, and diet of *Bothrops itapetiningae*, a species endemic to the Brazilian Cerrado. Habitat use was studied through active search techniques in several areas from July 1997 to July 2000. Diet, reproduction, activity, and sexual dimorphism were studied through the analysis of specimens deposited in Brazilian museums. Annual activity was inferred from collection records grouped by month and season. The specimens were sexed by direct observation of gonads and sexual dimorphism was assessed using morphological data. The reproductive cycle of the species was studied by analyzing the number of vitellogenic and nonvitellogenic follicles, ova, and embryos by month. The diet was determined by analyzing stomach and digestive tract contents. The species is a habitat specialist, associated with open cerrado grasslands, and is active more frequently during the rainy season (October to March). Males have longer tails whereas females have longer heads. The reproductive cycle is seasonal and probably biennial, with births (5.8 ± 2.9 embryos) occurring during the rainy season. Diet is of a generalist, but mammals are important items for both sexes and all age classes. *Bothrops itapetiningae* is among the smaller Brazilian pit vipers. Its low fecundity, high habitat specialization, and sensitivity to human disturbances, along with the high level of threat to its natural grassland habitat in the Brazilian Cerrado, makes this a potentially threatened snake. Knowledge of its biology is fundamental to conserving and managing this species.

RESUMO.—Apresentamos informações sobre uso de habitat, atividade, dimorfismo sexual, reprodução e dieta da cotiarinha (*Bothrops itapetiningae*), espécie endêmica do Cerrado Brasileiro. O uso de habitat foi estudado com base em diversas técnicas de buscas ativas ao longo de várias áreas de Cerrado, de julho de 1997 a julho de 2000. A atividade, reprodução, dimorfismo sexual e dieta foram estudadas através da análise de espécimes depositados em diversos museus brasileiros. O padrão anual de atividades de foi inferido a partir dos registros de coleta agrupados por mês e por estação. Os espécimes foram sexados pela observação direta das gônadas, dados morfológicos foram registrados para analisar o dimorfismo sexual. O ciclo reprodutivo da espécie foi estudado através da análise do número de folículos vitelogênicos e não vitelogênicos, óvulos e embriões por mês. Informações sobre dieta foi obtida por dissecação do estômago e trato digestivo. A espécie é especialista em habitat, associada a campos abertos de planalto e é ativa mais frequentemente durante a estação chuvosa (outubro a março). Os machos têm caudas mais longas, enquanto que as fêmeas têm cabeças maiores. O ciclo reprodutivo é sazonal com nascimentos ($5,8 \pm 2,9$ embriões) ocorrendo durante a estação chuvosa. A dieta é generalista, mas mamíferos são itens importantes na dieta de ambos os sexos e classes etárias. *Bothrops itapetiningae* possui baixa fecundidade, alta especialização habitat e alta sensibilidade a distúrbios humanos. Juntamente com o alto nível de ameaça de seus habitats naturais, torna-se uma prioridade conhecer melhor sua biologia para o seu manejo e conservação.

The viperid genus *Bothrops* (sensu Carrasco et al., 2012) includes 48 species distributed throughout the Americas from Mexico to Argentina (Campbell and Lamar, 2004; Carrasco et al., 2012). Brazil harbors the greatest diversity of the genus with about 25 species (Martins et al., 2001). Most species of *Bothrops* are forest dwellers but some of them, such as *Bothrops itapetiningae* Boulenger, 1907 (Fig. 1), are found exclusively in open habitats (Campbell and Lamar, 2004). *Bothrops itapetiningae* (“cotiarinha” or “jararaquinha-do-cerrado”) is a small terrestrial snake (Martins et al., 2001) endemic to the southern portion of the Brazilian Cerrado (Nogueira et al., 2011), the largest tract of Neotropical savanna. As for other squamates endemic to the Cerrado, natural history data for *B. itapetiningae* is scarce. Available data indicate mainly nocturnal activity (Nogueira, 2001; Sawaya et al., 2008) and frequent use of open grassland types of Cerrado habitats (“campo limpo,” “campo sujo,” “campo cerrado,” see Sawaya et al., 2008). As with all of its congeners, *B. itapetiningae* is viviparous but shows a relatively low fecundity, with only 3 to 11 embryos (Sawaya et al., 2008),

and has a generalist diet (Martins et al., 2002). However, detailed aspects of habitat use, reproduction (e.g., seasonality), and diet (e.g., main prey types, ontogenetic shifts in prey, prey sizes) remain poorly studied for this species.

The Cerrado has been affected by anthropogenic activities, such as agriculture and human settlement, to the point that original vegetation has been reduced to less than 50% of its former area (Ministério do Meio Ambiente, 2011). The Cerrado is included in the list of global priority areas for conservation (Myers et al., 2000) because of the high rates of habitat loss, species richness, and endemism. Basic information about the natural history of most reptilian species in the Cerrado is scarce (Colli et al., 2002; but see Nogueira et al., 2011). Thus, studies that aim to increase the knowledge about the biology of endemic species in the Cerrado are necessary, especially for conservation and management.

Given that finding snakes in nature is difficult, and that available information on the ecology and natural history for most snake species of Cerrado is scarce, preserved specimens from scientific collections are a highly valuable information source. We report the results of our specimen-based research and field studies to describe some aspects of habitat use, activity patterns, sexual dimorphism, reproduction, and diet of *B. itapetiningae*.

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FIG. 1. Young female of *Bothrops itapetiningae* (CHUNB 19270). See the dark tail characteristic of the species.

MATERIALS AND METHODS

Study Sites.—The Cerrado landscape is a mosaic of phytophysiognomies resulting from a diversity of soil types, topography, and climates occurring mostly between 300- and 1,600-m elevations (Ribeiro and Walter, 2008). Dominant phytophysiognomies are typical savannas (“cerrado”) with isolated trees in a matrix of grasses with some shrubs. Forest phytophysiognomies, dominated by tall trees, are restricted to valleys near streams and rivers or in places with more-fertile soils (Ribeiro and Walter, 2008). The main climate type is Aw in the Köppen classification (Peel et al., 2007). Mean annual temperature is 20°C (Nimer, 1989) and the annual rainfall (1,300–1,600 mm per year) is strongly seasonal and defines two main seasons: the dry season between April and September and the rainy season between October and March (Ribeiro and Walter, 2008).

Habitat Use.—Habitat use was studied based on time constrained searches (TCS; Martins and Oliveira, 1998), road sampling (Fitch, 1987), and opportunistic encounters (all the snakes found in situations other than searching activities) from July 1997 to July 2000. Previous results of field studies for other sympatric Cerrado pit vipers are available in Valdujo et al. (2002) and Nogueira et al. (2003). The TCS and opportunistic encounters took place in four localities within the range of *B. itapetiningae* (see Nogueira, 2001; Nogueira et al., 2003). Three sites are in central Brazil, near Brasília: Estação Ecológica Águas Emendadas (AEES), an ecological research station with approximately 10,000 ha at ~1,100 m elevation (15°33’S; 47°34’W); Reserva Área Alfa Cerrado (AACR), a Brazilian Navy training area with approximately 6,000 ha at ~1,150 m elevation (16°00’S; 47°56’W) (see Nogueira et al., 2005); and Reserva Biológica IBGE (RECOR IBGE) with approximately 1,350 ha at ~1,100 m elevation (15°57’S; 47°53’W). A fourth study site is located in southeastern Brazil near São Paulo: Estação Ecológica de Itirapina (IES) with approximately 2,300 ha at ~800 m elevation (22°15’S; 47°49’W). Detailed field data for IES were

supplied by R. J. Sawaya, pers. comm. (see also Sawaya et al., 2008).

The Cerrado areas in central Brazil around Brasília are dominated by typical savannas (“cerrado sensu stricto,” semi-open savannas with grasses), but open cerrado grasslands are also common on plateaus with gallery forests and wet grasslands also present on lower areas (Eiten, 1972).

Itirapina Ecological Station in southeastern Brazil is covered mostly by open grassy scrubland (campo sujo, grassland with scattered scrubs) with patches of wet grasslands, gallery forests, and open grassy savannas (campo cerrado, grassland with scattered trees).

Most snakes found in the field were collected except those in very poor condition (e.g., some road-kill animals). Collected specimens were fixed in 4% formaldehyde, preserved in 70% ethanol, and later deposited in scientific collections near study sites. For each individual found we recorded 1) time and date of encounter, 2) type of habitat and microhabitat, and 3) type of activity at first sight (moving, ambush, resting). The TCS were performed mainly at night, when higher encounter rates are usually obtained (Martins and Oliveira, 1998). Most searching activities were performed in recently burned areas or shortly after prescribed burns, as the removal of grassy cover by fire makes snakes more visible. At IBGE, some patches of natural vegetation were burned periodically as part of a study on the effects of fires on the Cerrado vegetation. During a TCS we searched for snakes above ground and in shelters (e.g., ground cavities, under termite mounds).

Specimens Analyzed.—Activity, sexual dimorphism, reproduction, and diet were studied based on the analysis of 188 specimens deposited in Coleção Herpetológica do Instituto Butantan (IB), Coleção Herpetológica da Universidade de Brasília (CHUNB), Coleção Herpetológica da Universidade Federal de Uberlândia (UFU), Museu de Zoologia da Universidade Estadual de Campinas (Unicamp), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu de História Natural Capão da Imbuia (MHNCI), and Coleção da Pontifícia Universidade Católica de Goiás (PUC-GO) (Appendix

1). Because not all of the 188 specimens were available for all analyses, the number of specimens analyzed was different among topics.

Activity.—The annual activity pattern of *B. itapetiningae* was inferred from the frequency of collection records that were grouped by month and by season (rainy/dry) for males, females, and juveniles. To test for differences in number of records of males, females, and juveniles among seasons, we performed multiple chi-square (χ^2) tests with 1,000 Monte Carlo randomizations. For each run we removed the variable (males, females, or juveniles) with the highest residuals until a nonsignificant result was obtained, aiming to identify which age class was responsible for observed differences. Records of males, females, and juveniles were compared between seasons using Student *t*-tests.

Sexual Dimorphism.—We sexed individuals by direct observation of the gonads, hemipenis, or by the presence of ovarian follicles. Each individual was also classified as adult or juvenile. Adult males had enlarged testis and/or convoluted deferens ducts while adult females had vitellogenic follicles and/or oviductal eggs (Shine, 1977; Shine, 1980). We considered all individuals with an SVL smaller than the smallest reproductive male to be juveniles. To analyze sexual dimorphism, we took the following measurements for males and females: tail length (TL), from the end of the tail to the opening of the cloaca; head length (HL), from the base of the maxilla to the end of the nostril; snout-vent length (SVL), from the end of the snout to the opening of the cloaca; and body circumference (BC). We measured TL and HL using a Mitutoyo® digital caliper (± 0.001 mm) and SVL and BC with a ruler (± 1 mm). Body mass (BM) was measured using a Pesola® spring scale (± 0.5 g) after draining the excess preservative from the specimen.

We performed all statistical analyses in R 2.14 software (R Development Core Team, 2011) with a significance level of 0.05. Prior to analyses we Z-standardized all morphological data to correct bias due to the use of different scales. Univariate outliers were identified with a significance level of 0.001 ($|z| > 3.2$; critical *z*) and removed (Callegari-Jacques, 2004). Data were then \log_{10} -transformed to conform to assumptions of normality. We also identified multivariate outliers using Cook's distance.

Some data were missing for SVL (1 record), HL (2), TL (11), BW (9), and BC (26) and were replaced using multivariate imputations by chained equations using the package *mice* in R 2.14 (Rubin, 2003; Zhang, 2003). To discriminate morphometric variation between size and shape, body size was defined as an isometric size variable with the scores of an isometric vector that considers that all body proportions remain equal throughout the ontogeny (Jolicoeur, 1963). To obtain the values of the size-free shape variables we used the method proposed by Burnaby (1966). To test if there is sexual dimorphism based on body size we performed an analysis of variance (ANOVA). We evaluated sexual dimorphism based on body shape through a logistic regression (general linear models) with sex as the dependent variable and morphometric variables as the independent variables (Tabachnick and Fidel, 2007). To select the best model and the variables that best explained the differences among sexes, we performed a stepwise manual selection based on the Akaike Information Criterion (AIC).

Reproduction.—We recorded the number of vitellogenic and nonvitellogenic follicles, number of ova, and number of embryos (as defined by Shine, 1988; Almeida-Santos and Salomão, 2002; Nogueira et al., 2003). We measured the

diameter (in the longitudinal axis) of the largest follicle, ovum, or embryo with a Mitutoyo digital caliper (± 0.001 mm).

We used multivariate imputations to estimate missing data for BM (5 individuals) and BC (14 individuals). Before performing multiple regression analysis we removed body mass as an independent variable because it was highly correlated with TL and BC ($r = 0.85$ for both variables). We used multiple regression analysis to test the association between SVL and BC with female fecundity. Fecundity was expressed as the number of vitellogenic follicles, number of ova, or number of embryos (Seigel and Ford, 1987). To estimate the extent of the reproductive period of *B. itapetiningae* we plotted the size of follicles, ova, and embryos by month, and to identify recruitment events we plotted SVL of males, females, and juveniles by month.

Diet.—We dissected stomachs and digestive tracts and identified all food contents (including food traces such as fur, feathers, scales, bones, teeth, etc.) under a stereomicroscope (Martins and Gordo, 1993). We verified the composition and frequency [(total items in category *i*/total items) \times 100] of each food item for pooled stomachs and separately by sex and age class (juveniles and adults). We calculated niche breadth for each sex and age class and niche overlap among sexes and age classes using R 2.14 software (packages *vegan* and *pgirmess*, respectively). Niche breadth was calculated using the standardized Levin's index (Colwell and Futuyma, 1971) whereas niche overlap was calculated using the overlap index proposed by Pianka (1986). We also tested if the proportion of empty stomachs was related to sex or age class by using χ^2 tests. The proportion of stomachs with and without food content was compared among seasons with a Fisher's exact test. The proportion of endothermic and ectothermic prey was compared among sexes, age classes, and seasons, also with Fisher's exact tests.

RESULTS

Habitat Use.—Six-hundred twenty-six man-hours of nocturnal TCS were performed: 403.60 man-hours in riparian habitats (gallery forest or wet grasslands) and 222.30 man-hours in open, interfluvial areas (campo sujo, campo cerrado, and "cerrado sensu stricto"). We found 11 individuals of *B. itapetiningae*, all in interfluvial, open grassland habitats (mostly campo sujo and campo cerrado). No individuals were found in riparian forested habitats. Encounter rates in interfluvial Cerrado areas were equivalent to 0.027 snakes per man-hour, or one snake found in each 37 man-hours of search.

Activity.—*Bothrops itapetiningae* was active year-round with an activity peak from the middle of the rainy season to the beginning of the dry season (January to April). Males and females were more often found during the dry season whereas juveniles were more common during the rainy season. The proportion of males, females, and juveniles among seasons was different from that expected by chance ($\chi^2_{[NA]} = 6.87$; $P = 0.03$), with juveniles responsible for the observed differences (males vs. females $\chi^2_{[NA]} = 0.41$; $P = 0.60$). There were no differences in the number of records of males among seasons ($t = 0.42$; $df = 150.58$; $P = 0.67$), but females and juveniles were recorded more often during the rainy season ($t = 2.04$; $df = 150.47$; $P = 0.04$; $t = -2.42$; $df = 147.75$; $P = 0.01$, respectively).

Sexual Dimorphism.—We measured 180 specimens (99 females and 81 males). The SVL of males varied from 164 to 510 mm (mean \pm SD: 368.59 \pm 62.14 mm) and of females from 200 to

TABLE 1. Raw and size-adjusted (in parenthesis) values for shape variables of *Bothrops itapetingae*. Size represents the isometric variable used to calculate the size-free shape variables.

Variable	Males (N = 81) (mean \pm SD)	Females (N = 99) (mean \pm SD)
Size	-0.64 \pm 1.64	0.55 \pm 2.21
Snout-vent length (SVL)	368.59 \pm 62.14 (-0.06 \pm 0.26)	442.29 \pm 99.98 (0.05 \pm 0.26)
Body mass (BM)	29.90 \pm 13.82 (-0.04 \pm 0.26)	57.04 \pm 33.33 (0.07 \pm 0.44)
Body circumference (BC)	45.38 \pm 8.6 (-0.13 \pm 0.39)	54.32 \pm 13.33 (0.08 \pm 0.45)
Tail length (TL)	49.35 \pm 8.62 (0.41 \pm 0.40)	47.17 \pm 10.83 (-0.34 \pm 0.37)
Head length (HL)	21.71 \pm 3.16 (-0.18 \pm 0.25)	25.98 \pm 4.74 (0.14 \pm 0.31)

613 mm (442.29 \pm 99.98 mm) (Table 1). Females were larger than males (standardized size for males: -0.65 \pm 1.63; adjusted size for females: 0.58 \pm 2.21; ANOVA: $F_{1,178} = 16.29$; $P < 0.001$). Logistic regression indicated differences in shape between males and females ($\chi^2_{177} = 123.59$; $P < 0.001$). The best model included TL and HL ($y = 5.12 - 1.39x - 0.30$) as the variables that best explain sexual dimorphism in shape. Males presented longer tails whereas females had larger heads. According to stepwise selection, TL is the more relevant variable in sexual dimorphism of *B. itapetingae*.

Reproduction.—Ninety-nine females carried from 3 to 11 embryos. The reproductive cycle of *B. itapetingae* is seasonal. Nonvitellogenic follicles were present year-round (Fig. 2). Vitellogenic follicles tended to increase in size from January to June. The largest ovum was found in early June. Embryos were found in October and December.

Juveniles were observed mostly in December and April (middle of the rainy season). The smallest female (228 mm SVL) was found in October whereas the largest female was found in April (613 mm). The smallest male (340 mm) was found in April and the largest (519 mm) in March. The smallest individual (185 mm) was collected in March (end of rainy season).

Multiple regression analysis showed a significant relation between fecundity, SVL, and BC ($F_{2,96} = 15.62$; $P < 0.001$). The best model selected contained only BC as the variable that best explained female fecundity ($y = 2.07x - 1.79$), showing that more-robust females are more fertile.

Diet.—We analyzed the diet of 190 specimens from which 141 (74.20%) had empty stomachs and guts. Only three stomachs had more than one food item. The diet of *B. itapetingae* is that of a generalist. The most frequent items were mammals (38.78%) followed by lizards (26.53%) and amphibians (24.49%), chilopods (8.16%), and birds (2.04%). Mammals (50%), amphibians (30%), and chilopods (20%) were the most common items for males ($N = 10$) whereas mammals (42.11%), amphibians (31.58%), and lizards (21.05%) were the most frequent items for females ($N = 19$). In juveniles ($N = 20$), the items most often found were lizards (45%), mammals (30%), and amphibians (15%) (Table 2). The proportion of ectothermic and endothermic prey items was not different among sexes (Fisher's exact test, $P = 0.65$), age classes (Fisher's exact test, $P = 1$), or seasons (Fisher's exact test, $P = 0.55$). Among age classes, the frequency of empty stomachs differed from that expected by chance ($\chi^2_{[NA]} = 21.45$; $P < 0.01$). Empty stomachs were more often found in adults, and females presented more empty stomachs than did males ($\chi^2_{[NA]} = 6.89$; $P = 0.01$). The proportion of stomachs with and without food content did not differ among seasons (Fisher's exact test, $P = 0.51$).

Dietary niche breadth for *B. itapetingae* was 0.62. We found no differences in niche breadth among sexes (males 0.41, females 0.52; $t = 0.10$; $df = 7.76$; $P = 0.92$) or age classes

(juveniles 0.53, adults 0.51; $t = 0.09$; $df = 7.78$; $P = 0.93$). Niche overlap was high both among sexes (0.90) and age classes (0.77).

DISCUSSION

Habitat Use.—All individuals of *B. itapetingae* were found in open interfluvial Cerrado grasslands and none in riparian forested areas. As with most other members of the *Bothrops alternatus* species group, *B. itapetingae* seems typical of open habitats. Previous descriptions of its habitat are vague, referring to "open fields and bushy areas" (Campbell and Lamar, 2004). However, based on field samples and opportunistic encounters, we describe its typical habitat as open, tabletop cerrado grasslands and savannas, locally known as campo sujo and campo cerrado, with a dense grassy cover and sparse, scattered arboreal stratum (see descriptions in Ratter, 1997), typical of interfluvial plateaus of the upper Paraná river basin (see Nogueira et al., 2011). During field searches in central Brazil near Brasilia, and in southeastern Brazil near São Paulo (Itirapina), 23 individuals of other species of *Bothrops* were found including four individuals of *B. alternatus* (Urutú cruzeiro); only in Itirapina, two snakes in riparian and two in interfluvial areas), six individuals of the "*B. neuwiedi*" (Jararaca pintada) species complex (see Silva and Rodrigues, 2008, all in interfluvial areas), and 13 individuals of *B. moojeni* (Caiçara; 12 of which were in riparian forests, see further data in Nogueira et al., 2003). Thus, sympatric *Bothrops* species from Cerrado can be found in different habitats but *B. itapetingae*, the most specialized in habitat requirements, is restricted to open, interfluvial cerrado grasslands.

Activity.—We found museum records of *B. itapetingae* in all months of the year. However, these records lack information on

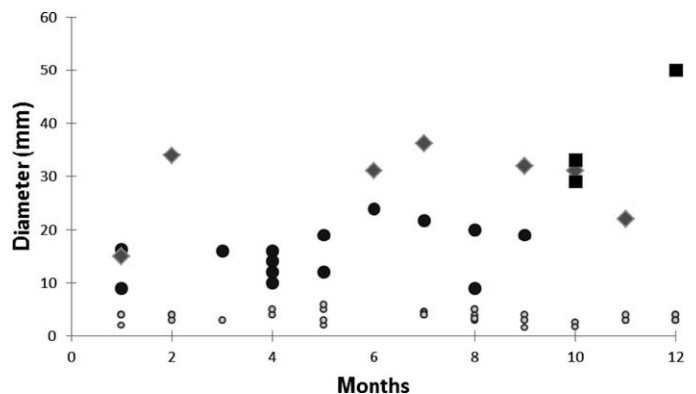


FIG. 2. Seasonal variation in follicle, ova, and embryo diameter from 99 *Bothrops itapetingae* females (small circles = not vitellogenic follicles; large circles = vitellogenic follicles; diamonds = ova; squares = embryos).

TABLE 2. Diet composition (frequency) of *Bothrops itapetiningae* by sex and age class.

Items	Frequency (%)			
	Pooled stomachs (N = 49)	Males (N = 10)	Females (N = 19)	Juveniles (N = 20)
Amphibians	24.49	30	31.58	15
Birds	2.04	-	-	5
Lizards	26.53	-	21.05	45
Mammals	38.78	50	42.11	30
Chilopods	8.16	20	5.26	5

how snakes were found or if they were active when collected (i.e., if they were moving, sheltered, or removed during soil digging by agricultural activities). Despite being recorded year-round, records were concentrated in the rainy season. Similar results were found by Sawaya (2003) at Itirapina, São Paulo. Several *Bothrops* species show a similar activity pattern, with few records during the dry season (May–June) and many records from mid to late warm rainy season (December to March/April) (Oliveira and Martins, 2002; Nogueira et al., 2003; Hartmann et al., 2004). Based on the presence of juveniles, births must occur in the rainy season. Males and females were found more often during the dry season, probably because of reduced motility due to colder temperatures and increased exposure when basking. Females of *B. itapetiningae*, gravid in this season, are less agile due to an increase in body mass and can be easily captured when basking (Shine, 1980; Hartmann et al., 2004).

Sexual Dimorphism.—The larger size of females is probably a widespread plesiomorphic condition in the genus *Bothrops*, as it is found in *B. asper* (Jararaca) (Solórzano and Cerdas, 1989), *B. jararaca* (Jararaca) (Sazima, 1992), *B. fonsecai* (Urutu) (Sazima and Manzani, 1998), *B. atrox* (Jararaca do norte) (Oliveira, 2003), *B. moojeni* (Nogueira et al., 2003), *B. pubescens* (Jararaca pintada) (Hartmann et al., 2004), *B. pauloensis* (Jararaca pintada) (Valdujo et al., 2002), and *B. alternatus* (Nunes et al., 2010).

Two major factors seem to influence sexual size dimorphism in snakes: agonistic behaviors that favor larger males or selective pressures for larger, more-fertile females. Thus, in some crotaline genera such as *Crotalus*, intrasexual combats are considered a selection factor favoring larger males (Carpenter et al., 1976). On the other hand, larger females can enhance fecundity by producing more eggs and/or embryos. As the reproductive success of females relies mainly on the number of offspring, larger females are positively selected (Shine, 1994). Moreover, smaller males could be favored by reduced metabolic costs and enhanced mobility, which in turn can increase success in avoiding predators, locating shelters, and finding mates (Shine, 1978). Because agonistic behaviors have not been documented for males of *B. itapetiningae*, selection based on female fertility can best explain the larger size of females (Shine, 1994; Campbell and Lamar, 2004).

In *B. itapetiningae*, males had longer tails and females had longer heads, as observed in other *Bothrops* species (Valdujo et al., 2002; Nogueira et al., 2003; Nunes et al., 2010). Longer tails in males are associated with the housing of hemipenes and their associated retractor muscles (King, 1989). Males with longer tails have larger hemipenes, thus enhancing their copulatory success, whereas males with shorter tails (due to predation or physical accidents) have smaller copulatory success (Shine et al., 1999).

Females with longer heads can feed on larger prey than can males, minimizing intersexual competition for food (Nogueira et al., 2003). Although females of *B. itapetiningae* have longer heads, we were not able to differentiate prey items consumed by sexes. However, differences in diet between sexes may be related to prey size and circumference, which we could not measure because most of the recovered food items were in an advanced degree of digestion. Another hypothesis regarding longer heads in females is related to the size of the venom glands. Some studies have shown that females of *B. alternatus* (Bauab et al., 1992), *B. atrox* (Beluomini et al., 1991), and *Bothrops leucurus* (Jararaca do rabo branco) (Biasi et al., 1977) produce a larger volume of venom than do males.

Reproduction.—Mean clutch size for *B. itapetiningae* (5.8 ± 2.9 ova/embryos) was smaller than the clutch sizes known for most snakes (Sazima, 1992), smaller than the mean clutch size known for Viperidae (Seigel and Ford, 1987), and also smaller than those of other species of *Bothrops* such as *B. moojeni* (15.6) (Nogueira et al., 2003), *B. jararacussu* (Jararacuçu; 13–37) (Marques and Sazima, 2004), *B. jararaca* (3–34) (Sazima, 1992), *B. atrox* (33) (Hoge and Federsoni, 1977), *B. alternatus* (13) (Araújo, 1978), *B. leucurus* (12) (Lira-da-Silva et al., 1994), *B. pubescens* (11) (Hartmann et al., 2004), *B. neuwiedi* (6,8) (Alves et al., 1998), and *B. pauloensis* (9,27) (Valdujo et al., 2002).

As found for most reptiles (Vitt and Caldwell, 2009) and for all viviparous Brazilian snakes (Pizzatto et al., 2007), the reproductive cycle of *B. itapetiningae* is seasonal. This is also a common reproductive pattern for many tropical reptiles, including those from the Cerrado where the climatic seasonality seems coupled with seasonal reproductive cycles (Colli et al., 1997). Although reptiles from nonseasonal climates tend to have continuous reproduction, all Brazilian *Bothrops* studied thus far, including those from Amazonia and Atlantic forest (such as *B. atrox* and *B. jararaca*), showed seasonal reproduction (Pizzatto et al., 2007), suggesting a strong phylogenetic influence.

We found females containing nonvitellogenic follicles year-round, along with some females containing vitellogenic follicles, which suggest a biennial reproductive cycle (Pizzatto et al., 2007). Several other viperid snakes present biennial cycles including *B. jararaca* (Almeida-Santos and Orsi, 2002), *Crotalus durissus* (Cascavel) (Almeida-Santos et al., 2004), and *B. pauloensis* (Valle and Brites, 2008). We found embryos between October and December with births occurring in the rainy season. The increase in body temperatures and metabolic rates of snakes during the rainy season speeds the development of embryos and reduces the incidence of anomalies (Vinegar, 1974).

For most snake species, fecundity seems to be the highest selective pressure responsible for the increase in size of females (Shine, 1994) and can be variable throughout a species distribution, probably according to availability of food (Vitt and Vangilder, 1983).

We also found a significant relationship between fecundity and SVL, and between fecundity and body circumference, as found in other viperid species (Janeiro-Cinquini and Leinz, 1990; Valdujo et al., 2002; Janeiro-Cinquini, 2004). Body circumference was the variable that best explained female fecundity, probably because it is an adaptive characteristic of gestation and morphology of the reproductive system.

Diet.—The number of empty stomachs in our study was related to ontogeny and sex. We found more adults than juveniles of *B. itapetiningae* with empty stomachs. The high metabolic rate associated with development, and the inability of capturing large prey items, could force juveniles to feed more

frequently than adults, which eat larger and more-caloric prey and can wait longer periods of time without feeding (Pough et al., 2008). We also found more females than males with no gut contents, possibly due to the fact that gravid females could not feed during this stage. Snakes carrying embryos, or that are at the end of secondary vitellogenesis, rarely feed (Shine, 1977, 1980), probably due to a reduction of space in the body cavity and a reduced hunting ability (Shine, 1980). Males, on the other hand, tend to increase their feeding frequency during or before spermatogenesis (Pizzatto et al., 2006).

As observed for *B. pauloensis* (Valdujo et al., 2002), the diet of *B. itapetiningae* did not differ among seasons (rainy and dry), indicating that the species feeds on prey that are active year round and/or share the same microhabitats. We found no relation between sex, ontogeny, or season with the occurrence of endo- or ectothermic prey. Previous to our study it was suggested that *B. itapetiningae* may have an intermediate diet between generalists and specialists (Nogueira, 2001). *Bothrops itapetiningae* has a generalist diet, like most *Bothrops* species, and feeds on similar food items (mammals, lizards, amphibians, chilopods, and birds) (Nogueira, 2001; Martins et al., 2002; Valdujo et al., 2002; Sawaya et al., 2008), which may reflect an ancestral trait of the genus. Although a generalist *B. itapetiningae* feeds mainly on rodents, as do other species of the *B. alternatus* group, (i.e., *B. cotiara* [Cotiara], *B. fonsecai*, and *B. alternatus*), and of the *B. neuwiedi* group (*B. neuwiedi*) who are mammal specialists (Nogueira, 2001; Martins et al., 2002; Sawaya, 2003; Nunes et al., 2010).

The predominance of rodents in the diet of *B. itapetiningae* may reflect the high abundance, richness, and year-round activity of Cerrado rodents (Salomão et al., 1995; Marinho-Filho et al., 2002). The full specialization of *B. itapetiningae* on rodents may also be hindered by the small body size of this snake species. On the other hand, the high proportion of rodents in gut contents of a generalist species may reflect prey availability, predation costs, and body size of the predator (Martins et al., 2002). Lizards and amphibians were also important food items in the diet of *B. itapetiningae*. The conspicuous presence of these prey items in the diet of a generalist snake could also be explained by prey availability in the environment (Shine, 1991). Amphibians are harmless prey that could be easily seized by a snake without threat of injury (Martins et al., 2002). Accordingly, they are common prey items of South American snakes (Vitt and Vangilder, 1983). Chilopods were the unique invertebrate taxa found in the diet of *B. itapetiningae* and were also present in the diet of other *Bothrops* such *B. moojeni*, *B. pauloensis*, *B. atrox*, *B. hyoprurus* (Jararaca bicuda), *B. erythromelas* (Jararaca da seca), *B. pubescens*, *B. jararaca*, *B. insularis* (Jararaca ilhoa), *B. brazili* (Jararaca) and *B. jararacussu* (Nogueira, 2001; Martins et al., 2002; Valdujo et al., 2002; Sawaya et al., 2008). As *B. itapetiningae* feeds mainly on rodents, it is usually considered a sit-and-wait forager (Sawaya et al., 2008). However, the high proportion of amphibians and lizards found in gut contents of *B. itapetiningae* could indicate that the species can ambush active lizards and amphibians and/or the species can forage actively in opportunistic incursions (e.g., when moving in search of refuges or mates or during thermoregulatory behavior).

Diet was not influenced by ontogeny or sex, as indicated by the lack of significant differences in niche breadth among sexes and age classes and by the high values of niche overlap between males, females, juveniles, and adults. The lack of ontogenetic changes in the diet of *B. itapetiningae* seems to be a derived characteristic in the *B. alternatus* group (Nogueira, 2001), as no

Bothrops species in this group shows changes in diet during ontogeny (Martins et al., 2002). Ontogenetic changes in diet seem to be related to the caudal luring behavior of juveniles that is lost in adults. Caudal luring is a widespread strategy in juveniles of many *Bothrops* (i.e., *B. atrox*, *B. bilineatus* [Bico de papagaio], *B. jararaca*, *B. jararacussu*, and *B. moojeni*) that use their white tails as bait for attracting amphibians and lizards (Sazima, 1991, 1992; Marques, 1998; Nogueira et al., 2003). The lack of caudal luring in some crotaline snakes has been suggested as an explanation for the absence of ontogenetic changes in diet (Heatwole and Davison, 1976). However, as both adults and juveniles of *B. itapetiningae* have a dark tail and feed on lizards and amphibians, caudal luring is possibly present in this species. Although this behavior has not been registered yet for *B. itapetiningae*, this pedomorphic trait seems to be present in other *Bothrops* species such as *B. bilineatus* (Greene and Campbell, 1972) and possibly *B. insularis* (Martins et al., 2002). An ontogenetic shift in diet is also present in the sister group of *Bothrops* and, thus, it seems to have been lost in the *B. alternatus* group and at least one time in the *B. neuwiedi* group (Martins et al., 2002).

Overall, most of the natural history traits of *B. itapetiningae* (e.g., seasonal reproduction, nocturnal habits, and biennial reproduction) seem to reflect plesiomorphic conditions widespread in *Bothrops*. However, our data reveal some distinct characteristics closely related to snakes of the *B. alternatus* group such as the predominant use of open areas, the high frequency of mammalian prey, and the lack of ontogenetic dietary shifts. Among the members of the *B. alternatus* group, *B. itapetiningae* differs in some major ecological traits, such as its smaller body size, which may have prevented its complete specialization on a diet of mammals and constrained its fecundity.

Bothrops itapetiningae is among the smaller Brazilian pit vipers. Its low fecundity, high habitat specialization, relative rarity, and sensitivity to human disturbances (Nogueira, 2001; Sawaya et al., 2008), along with the high level of threat to natural habitats in the Brazilian Cerrado (Ministério do Meio Ambiente, 2011), indicate that this snake species is potentially under threat. However, conservation assessment of this snake and other poorly studied Neotropical reptiles remain hampered by lack of basic natural history data. A better understanding of basic biological aspects of *Bothrops itapetiningae* is fundamental for the conservation of this poorly studied and unique Neotropical pit viper.

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LITERATURE CITED

- ALMEIDA-SANTOS, S. M., AND A. M. ORSI. 2002. Ciclo Reprodutivo de *Crotalus durissus* e *Bothrops jararaca* (Serpentes, Viperidae): morfologia e função do oviduto. *Revista Brasileira de Reprodução Animal* 26:109–112.

- ALMEIDA-SANTOS, S. M., AND M. G. SALOMÃO. 2002. Reproduction in Neotropical pitvipers, with emphasis on species of the genus *Bothrops*. In G. W. Schuett, M. Hoggren, M. E. Douglas, and H. W. Greene (eds.), *Biology of the Vipers*, pp. 445–462. Eagle Publishing, USA.
- ALMEIDA-SANTOS, S. M., F. M. F. ABDALLA, P. F. SILVEIRA, N. YAMANOUYE, M. C. BRENO, AND M. G. SALOMÃO. 2004. Reproductive cycle of the Neotropical *Crotalus durissus terrificus*: I. Seasonal levels and interplay between steroid hormones and vasotocinase. *General and Comparative Endocrinology* 139:143–150.
- ALVES, M. L. M., M. LEITÃO-DE-ARAÚJO, AND E. CABERLON. 1998. Atividade reprodutiva de *Bothrops neuwiedi* em cativeiro (Serpentes, Viperidae). *Iheringia, Série Zoológica* 84:185–191.
- ARAÚJO, M. L. 1978. Notas sobre ovos de serpentes (Boidae, Colubridae, Elapidae e Viperidae). *Iheringia, Série Zoológica* 51:9–37.
- BAUAB, F. A., Y. IWASHIMA, V. L. C. BRITES, J. C. CURY, AND W. T. VICTORINO. 1992. Estudo comparativo da produção máxima de peçonha e inquérito bacteriológico bucal em serpentes Viperidae, Uberlândia Anais do Congresso Científico da UFU:110.
- BELUOMINI, H. E., P. BIASI, G. PUORTO, W. FERNANDES, AND A. L. DOMINGUES. 1991. Amostras da população de *Bothrops atrox* (Linnaeus, 1758) apreciadas nas quantidades de veneno obtidas e dados ecológicos, Belém. *Boletim do Museu Paraense Emílio Goeldi, Nova Serie, Zoológica* 7:53–69.
- BIASI, P., H. E. BELUOMINI, AND W. FERNANDES. 1977. Quantidade de veneno obtidas na extração de serpentes *Bothrops pradoi* (Hoge, 1948) (Serpentes, Viperidae, Crotalinae). *Memórias do Instituto Butantan* 40/41:155–166.
- BOULENGER, G. A. 1907. Description of a new pit viper from Brazil. *Annals and Magazine of Natural History, 7th Series* 20:338.
- BURNABY, T. P. 1966. Growth-invariant discriminant functions and generalized distances. *Biometrics* 22:96–110.
- CALLEGARI-JACQUES, S. M. 2004. *Bioestatística: Princípios e Aplicações*. Artmed, Brasil.
- CAMPBELL, J. A., AND W. W. LAMAR. 2004. *The Venomous Reptiles of the Western Hemisphere, Volumes I–II: 1st*. Cornell University Press, USA.
- CARPENTER, C. C., J. C. GILLINGHAM, AND J. B. MURPHY. 1976. The combat ritual of the rock rattlesnake (*Crotalus lepidus*). *Copeia* 4:764–780.
- CARRASCO, P. A., C. I. MATTONI, G. C. LEYNAUD, AND G. J. SCROCCHI. 2012. Morphology, phylogeny and taxonomy of South American bothropoid pitvipers (Serpentes, Viperidae). *Zoologica Scripta* 41:109–124.
- COLLI, G. R., A. K. PERES JR., AND M. G. ZATZ. 1997. Foraging mode and reproductive seasonality in tropical lizards. *Journal of Herpetology* 31:490–499.
- COLLI, G. R., R. P. BASTOS, AND A. F. B. ARAÚJO. 2002. The character and dynamics of the Cerrado herpetofauna. In P. S. Oliveira and R. J. Marquis (eds.), *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*, pp. 223–241. Columbia University Press, USA.
- COLWELL, R. K., AND D. J. FUTUYMA. 1971. On the measurement of niche breadth and overlap. *Ecology* 52:567–576.
- EITEN, G. 1972. The Cerrado vegetation of Brazil. *Botanical Review* 38: 201–341.
- FITCH, H. S. 1987. Collecting and life-history techniques. In R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 143–164. MacMillan Publishing Co., USA.
- GREENE, H. W., AND J. A. CAMPBELL. 1972. Notes on the use of caudal lures by arboreal green pit vipers. *Herpetologica* 28:32–34.
- HARTMANN, M. T., O. A. V. MARQUES, AND S. M. ALMEIDA-SANTOS. 2004. Reproductive biology of the southern Brazilian pitviper *Bothrops neuwiedi pubescens* (Serpentes, Viperidae). *Amphibia-Reptilia* 25:77–85.
- HEATWOLE, H., AND E. DAVISON. 1976. A review of caudal luring in snakes with notes on its occurrence in Saharan sand viper, *Cerastes vipera*. *Herpetologica* 32:332–336.
- HOGUE, A. R., AND P. A. FEDERSONI. 1977. Observações sobre uma ninhada de *Bothrops atrox* (Linnaeus, 1758) (Serpentes: Viperidae: Crotalinae). *Memórias do Instituto Butantan* 40/41:19–36.
- JANEIRO-CINQUINI, T. R. F. 2004. Variação anual do sistema reprodutor de fêmeas de *Bothrops jararaca* (Serpente, Viperidae). *Iheringia, Série Zoológica* 94:325–328.
- JANEIRO-CINQUINI, T. R. F., AND F. F. LEINZ. 1990. Body size-litter relationships and some characteristics of litters in *Bothrops jararaca*. *Bulletin of the Chicago Herpetological Society* 25:84–85.
- JOLICOEUR, P. 1963. The multivariate generalization of the allometry equation. *Biometrics* 19:497–499.
- KING, R. B. 1989. Sexual dimorphism in snake tail-length: sexual selection, natural selection or morphological constraint? *Biological Journal of the Linnean Society* 38:133–154.
- LIRA-DA-SILVA, R. J., L. L. CASAIS-E-SILVA, I. B. QUEIROZ, AND T. B. NUNES. 1994. Contribuição à biologia de serpentes da Bahia, Brasil. I. Vivíparas. *Revista Brasileira de Zoologia* 11:187–193.
- MARINHO-FILHO, J., F. H. G. RODRIGUES, AND K. M. JUAREZ. 2002. The Cerrado mammals: diversity, ecology, and natural history. In P. S. Oliveira and R. J. Marquis (eds.), *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*, pp. 266–286. Columbia University Press, USA.
- MARQUES, O. A. V. 1998. *Composição Faunística, História Natural e Ecologia de Serpentes da mata Atlântica, na Região da Estação Ecológica Juréia-Itatins, São Paulo, SP*. Ph.D. diss., Universidade de São Paulo, Brasil.
- MARQUES, O. A. V., AND I. SAZIMA. 2004. História natural dos répteis da Estação Ecológica Juréia-Itatins. In O. A. V. Marques and W. Duleba (eds.), *Estação Ecológica Juréia-Itatins: Ambiente Físico, Flora e Fauna*, pp. 257–277. Holos Editora, Brasil.
- MARTINS, M., AND M. GORDO. 1993. *Bothrops atrox* (Common Lancehead). *Diet. Herpetological Review* 24:151–152.
- MARTINS, M., AND M. E. OLIVEIRA. 1998. Natural history of snakes in forests of the Manaus region, central Amazonia. *Herpetological Natural History* 6:78–150.
- MARTINS, M., M. S. ARAUJO, 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* 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. Schuett, M. Höggren, and H. W. Greene (eds.), *Biology of the Vipers*, pp. 307–328. Biological Sciences Press, USA.
- MINISTÉRIO DO MEIO AMBIENTE. 2011. Monitoramento do desmatamento nos biomas brasileiros por satélite: monitoramento do bioma Cerrado, 2008–2009: an online reference [Internet]. Available from: http://www.mma.gov.br/estruturas/sbf_chm_rbbio/_arquivos/relatoriofinal_cerrado_2010_final_72_1.pdf. Archived by WebCite at <http://www.webcitation.org/6FuKrwk7p> on 15 April 2013.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- NIMER, E. 1989. *Climatologia do Brasil*. Fundação IBGE, Brasil.
- NOGUEIRA, C. C. 2001. *Ecologia Histórica de Bothrops spp.* (Serpentes: Viperidae: Crotalinae) simpátricas no Cerrado. MSc. thesis, Universidade de São Paulo, Brasil.
- NOGUEIRA, C. C., R. J. SAWAYA, AND M. MARTINS. 2003. Ecology of the pitviper, *Bothrops moojeni*, in the Brazilian Cerrado. *Journal of Herpetology* 37:653–659.
- NOGUEIRA, C., P. H. VALDUJO, AND F. G. R. FRANÇA. 2005. Habitat variation and lizard diversity in a Cerrado area of central Brazil. *Studies on Neotropical Fauna and Environment* 40:105–112.
- NOGUEIRA, C. C., S. RIBEIRO, G. C. COSTA, AND G. R. COLLI. 2011. Vicariance and endemism in a Neotropical savanna hotspot: distribution patterns of Cerrado squamate reptiles. *Journal of Biogeography* 38: 1907–1922.
- NUNES, S. F., I. L. KAEFER, P. T. LEITE, AND S. Z. CECHIN. 2010. Reproductive and feeding biology of the pitviper *Rhinocerocephalus alternatus* from subtropical Brazil. *The Herpetological Journal* 20:31–39.
- OLIVEIRA, M. E., AND M. MARTINS. 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, M. E. E. S. 2003. *História Natural de Jararacas Brasileiras do Grupo Bothrops atrox* (Serpentes: Viperidae). Ph.D. diss., Universidade Estadual Paulista, Brasil.
- PEEL, M. C., B. L. FINLAYSON, AND T. A. MCMAHON. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* 11:1633–1644.
- PIANKA, E. R. 1986. *Ecology and Natural History of Desert Lizards. Analyses of the Ecological Niche and Community Structure*. Princeton University Press, USA.
- PIZZATTO, L., R. M. HADDAD, AND S. M. ALMEIDA-SANTOS. 2006. Male-male ritualized combat in the Brazilian rainbow boa *Epicrates cenchria crassus*. *Herpetological Bulletin* 95:16–20.
- PIZZATTO, L., S. ALMEIDA-SANTOS, O. MARQUES, L. NASCIMENTO, AND M. OLIVEIRA. 2007. Biologia reprodutiva de serpentes brasileiras. In L. B.

- Nascimento and M. E. Oliveira (eds.), *Herpetologia no Brasil II*, pp. 201–221. Sociedade Brasileira de Herpetologia, Brasil.
- POUGH, F. H., J. B. HEISER, AND C. M. JANIS. 2008. *A Vida dos Vertebrados*. Editora Atheneu, Brasil.
- R DEVELOPMENT CORE TEAM. 2011. *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available from: <http://www.R-project.org>. ISBN 3-900051-07-0.
- RATTER, J. 1997. The Brazilian Cerrado vegetation and threats to its biodiversity. *Annals of Botany* 80:223–230.
- RIBEIRO, J. F., AND B. M. T. WALTER. 2008. As principais fitofisionomias do bioma Cerrado. In S. M. Sano, S. P. Almeida, and J. F. Ribeiro (eds.), *Cerrado: Ecologia e Flora*, pp. 151–212. Embrapa Cerrados, Brasil.
- RUBIN, D. B. 2003. Discussion on multiple imputation. *International Statistical Review* 71:619–625.
- SALOMÃO, M. G., S. M. ALMEIDA-SANTOS, AND G. PUERTO. 1995. Activity pattern of the rattlesnake *Crotalus durissus* (Viperidae: Crotalinae): feeding, reproduction and snakebite. *Studies on Neotropical Fauna Environment* 30:101–106.
- SAWAYA, R. J. 2003. *História Natural e Ecologia das Serpentes de Cerrado da Região de Itirapina, SP*. Ph.D. diss., Universidade Estadual de Campinas, Brasil.
- SAWAYA, R. J., O. A. V. MARQUES, AND M. MARTINS. 2008. Composition and natural history of a Cerrado snake assemblage at Itirapina, São Paulo state, southeastern Brazil. *Biota Neotropica* 8:127–149.
- SAZIMA, I. 1991. Caudal luring in two Neotropical pitvipers, *Bothrops jararaca* and *B. jararacussu*. *Copeia* 1991:245–248.
- . 1992. Natural history of the jararaca pitviper, *Bothrops jararaca*, in South-eastern Brazil. In J. A. Campbell and E. D. Brodie (eds.), *Biology of the Pitvipers*, pp. 199–216. Tyler Selva, USA.
- SAZIMA, I., AND P. R. MANZANI. 1998. *Bothrops fonsecai* (Fonseca's Lancehead). Reproduction and size. *Herpetological Review* 29:102–103.
- SEIGEL, R. A., AND N. B. FORD. 1987. Reproductive ecology. In R. A. Seigel, J. T. Collins, and S. S. Novak (Eds.), *Snakes, Ecology and Evolutionary Biology*, pp. 210–252. McMillan Publishing Company, USA.
- SHINE, R. 1977. Reproduction in Australian elapid snakes II. Female reproductive cycles. *Australian Journal of Zoology* 25:655–666.
- . 1978. Sexual size dimorphism and male combat in snakes. *Oecologia* 33:269–277.
- . 1980. "Costs" of reproduction in reptiles. *Oecologia* 46:92–100.
- . 1988. Food habits and reproductive biology of small Australian snakes of the genera *Uroechis* and *Suta* (Elapidae). *Journal of Herpetology* 22:307–315.
- . 1991. Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *American Naturalist* 12:103–122.
- . 1994. Sexual dimorphism in snakes revised. *Copeia* 1994:326–346.
- SHINE, R., M. M. OLSSON, I. T. MOORE, M. P. LEMASTER, AND R. T. MASON. 1999. Why do males snakes have longer tails than females? *Proceedings of the Royal Society of London* 266:2147–2151.
- SILVA, V. X., AND M. T. RODRIGUES. 2008. Taxonomic revision of the *Bothrops neuwiedi* complex (Serpentes, Viperidae) with description of a new species. *Phyllomedusa* 7:45–90.
- SOLÓRZANO, A., AND L. CERDAS. 1989. Reproductive biology and distribution of the terciopelo, *Bothrops asper* Garman (Serpentes: Viperidae), in Costa Rica. *Herpetologica* 45:195–207.
- TABACHNICK, B. G., AND L. S. FIDEL. 2007. *Using Multivariate Statistics*. Pearson Education, USA.
- VALDUJO, P. H., C. C. NOGUEIRA, AND M. MARTINS. 2002. Ecology of *Bothrops neuwiedi pauloensis* (Serpentes: Viperidae: Crotalinae) in the Brazilian Cerrado. *Journal of Herpetology* 36:169–176.
- VALLE, L. A., AND C. L. V. BRITES. 2008. Nomes populares e aspectos ecológicos de *Bothrops pauloensis* (Amaral 1925) em áreas antropizadas do Triângulo e Alto Paranaíba, Minas Gerais. *Revista Brasileira de Zoociências* 10:155–161.
- VINEGAR, A. 1974. Evolutionary implications of temperature induced anomalies of development on snake embryos. *Herpetologica* 30:72–74.
- VITT, L. J., AND L. D. VANGILDER. 1983. Ecology of a snake community in northeastern Brazil. *Amphibia-Reptilia* 4:273–296.
- VITT, L. J., AND J. P. CALDWELL. 2009. *Herpetology: An Introductory Biology of Amphibians and Reptiles*. Academic Press, USA.
- ZHANG, P. 2003. Multiple imputation: theory and method. *International Statistical Review* 71:581–592.

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APPENDIX 1

Specimens Examined.—Coleção da Pontifícia Universidade Católica de Goiás: CEPB 2863. Museu de História Natural Capão da Imbuia, Curitiba: MHNCI 4127. Museu de Zoologia da Universidade de São Paulo: MZUSP 1437, MZUSP 13931. Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso": ZUEC REP 3105, ZUEC REP 3099, ZUEC REP 3104. Coleção da Universidade Federal de Uberlândia: UFU 206, UFU 224, UFU 564, UFU 616, UFU 1012. Coleção Herpetológica da Universidade de Brasília: CHUNB 03590, CHUNB 03591, CHUNB 14342, CHUNB 19270, CHUNB 19272, CHUNB 19273, CHUNB 24901, CHUNB 28878, CHUNB 32642, CHUNB 49445, CHUNB 49450, CHUNB 52365, CHUNB 57440. Coleção do Instituto Butantan: IB9, IB18, IB19, IB20, IB456, IB514, IB645, IB878, IB1309, IB1340, IB1497, IB1602, IB1609, IB1612, IB1629, IB1810, IB1833, IB2689, IB2723, IB2740, IB2741, IB2742, IB3259, IB3539, IB3592, IB3718, IB3780, IB3782, IB3784, IB3785, IB4409, IB4532, IB4721, IB4772, IB4856, IB4866, IB5190, IB5227, IB5295, IB5541, IB5589, IB5717, IB5821, IB5863, IB5954, IB5991, IB6060, IB6182, IB6255, IB6793, IB6826, IB7260, IB7297, IB7328, IB7340, IB7341, IB7355, IB7426, IB7427, IB7457, IB7710, IB7711, IB7779, IB7813, IB7843, IB7889, IB8291, IB8436, IB8437, IB8577, IB8714, IB9122, IB9243, IB9396, IB9434, IB9461, IB9474, IB9584, IB9675, IB9678, IB9679, IB9685, IB9688, IB9697, IB9698, IB9723, IB9729, IB9741, IB9838, IB9875, IB9926, IB9937, IB9940, IB9961, IB9963, IB9965, IB9974, IB9975, IB9978, IB9995, IB10350, IB10374, IB10375, IB10668, IB11745, IB12184, IB12185, IB12632, IB12706, IB13136, IB15152, IB15302, IB15774, IB15775, IB15865, IB16645, IB16883, IB16934, IB17028, IB17029, IB17396, IB17859, IB20619, IB26722, IB29313, IB30591, IB32308, IB32386, IB33443, IB33607, IB34492, IB37584, IB40319, IB40334, IB40465, IB41120, IB41777, IB43113, IB44009, IB45538, IB45932, IB48224, IB48349, IB49143, IB49647, IB51621, IB52830, IB53424, IB57097, IB57098, IB57099, IB57431, IB57718, IB57731, IB61651, IB61652, IB61653, IB61655, IB61656, IB61657, IB61658, IB403m, IB403p.